
# Eye movements and the maximization of value

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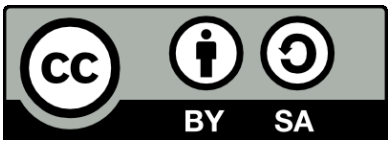

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# Contents

# 1 Summary

Only the central region of the retina, the fovea, can provide us with high-acuity details of our visual environment. In the periphery however, resolution fades away with increasing eccentricity. As a consequence, humans and other animals with a foveated visual system move their eyes to redirect their gaze towards objects of interest. And with each saccadic eye movement, we choose a different region of the visual field for high-acuity processing. In the recent decades, the eye movement system has thus evolved as a role model to study decision making (Glimcher, 2003), which is also because the oculomotor system is sensitive to valuation processes. Moreover, our eye movements are tightly linked to visual perception, because where we look determines what we see and every eye movement poses a major challenge to the visual system as it shifts the whole visual image on the retina. In three studies, this dissertation project examined whether the eye movement system can adjust saccade latencies to maximize informational and motivational value and whether the visual system can maximize all the information available despite making eye movements.

The first study investigated whether the eye movement system is sensitive to the information that can be gained by executing an eye movement. Participants saccaded to a peripherally appearing target and perform a perceptual task. By exchanging the target while the saccade was in flight, we could independently manipulate the pre-saccadic peripheral and the post-saccadic foveal visibility and thus create conditions where participants either lost or gained information by making an eye movement. In the loss condition, the probability of correctly identifying the target increased with saccade latency because participant could benefit longer from high resolution peripheral vision. The opposite pattern was observed in the gain condition. However, eye movement latencies did not differ no matter whether participants could gain or lose information and thus could not maximize the all the information available. Instead, latencies decreased with the probability that visual information at the saccade target was task-relevant, suggesting that saccade eye movements are influenced by the motivation to foveate task-relevant information, but not by the information that can be gained by saccade execution.

In Study II, we tested whether the visual system is able to integrate pre-saccadic peripheral and post-saccadic foveal information and whether it weighs the incoming visual information according to its reliability, that is, according to how well something can be seen. This optimal

integration would minimize the perceptual uncertainty and thus maximize all the information available to the visual system. For every individual, we separately measured discrimination performance in the fovea and the periphery. Using maximum-likelihood integration (Ernst & Bülthoff, 2004), we predicted the optimal weight given to peripheral information as well as the optimal uncertainty associated with the trans-saccadic percept. Both, in terms of weighting and uncertainty, trans-saccadic performance was not distinguishable from optimality. We thus could show that the visual system is able to integrate information across saccades and that it is close to optimal in doing so. This highlights that the visual system is able to maximize all the visual information available despite making eye movements.

Study III investigated whether the influence of expected motivational value on saccades (Milstein & Dorris, 2007, 2011) can only be found in contexts where participants additionally have to choose between multiple rewarded targets. We recorded saccade latencies to rewarded targets differing in reward and manipulated the proportion of interleaved choices within one block. In choice-trials, two targets were displayed and participants could choose between the two to obtain the corresponding reward. Without choices present, we found no evidence for single target saccades to be affected by reward. When choices were interleaved, latencies to less rewarded targets were delayed and the magnitude of this delay increased with the proportion of choices. This delay was elicited by the expectation of an upcoming choice-trial as well as inter-trial priming: After a choice, saccadic reactions to the non-chosen target were delayed. We thus could show that there is no direct relationship between expected motivational value on the one hand and saccade latencies on the other hand. Rather, this relationship only persists in contexts where humans can maximize their reward outcome by preferring one target over the other.

In sum, the present dissertation shows that there is no direct relationship between saccade latencies on the one hand and motivational value (Study III) or informational value (Study I) on the other hand. Instead, saccade latencies are sensitive to the probability that information acquired at the saccade target becomes task-relevant (Study I) and the preference of one target over the other (Study III). For perception we could show that the visual system can optimally integrate information about saccades and thus that vision does not correspond to disconnected snapshots, but rather to an integrated stream of continuous information (Study II).

# 2 Introduction

The world surrounding us is full of visual details. Some of those visual details might be relevant to successfully interact with our environment, others are interesting or just beautiful to look at. Yet, we can never process all visual information at the same time, because of the foveated nature of our visual system. Only a small region of the retina, the fovea, is capable of processing visual information with high acuity. Outside the fovea, visual acuity declines rapidly with increasing eccentricity. As a consequence, we have to shift our gaze and reorient our foveae towards those visual details which we consider relevant or interesting. These gaze shifts are achieved by saccade eye movements. Saccades are quick movements of the eye which, depending on their amplitude, last between 20-80 ms and can reach an angular speed of up to 900 deg/s (Bahill, Clark, & Stark, 1975). On average, humans perform around two to three saccades per second, each time choosing a different object or region within the visual field for high acuity processing. Oversimplified, visual perception can therefore be described as a constant change between phases when the eyes are moving and phases when they are fairly still, called fixations. Because vision is mostly suppressed during saccade eye movements (Zuber & Stark, 1966), new visual information is mainly acquired during fixations. Thus, during fixations, foveal vision is used to process information in detail whereas peripheral vision simultaneously selects the next saccade target (Ludwig, Davies, & Eckstein, 2014).

There is an increasing number of computational models which aim to predict gaze based on the saliency of an image (Itti & Koch, 2000; Zhang, Tong, Marks, Shan, & Cottrell, 2008). Other models additionally emphasize the participants' task (Navalpakkam & Itti, 2005; Rothkopf, Ballard, & Hayhoe, 2007) or the abilities of the visual system (Najemnik & Geisler, 2005, 2008; Renninger, Verghese, & Coughlan, 2007). Behavioral studies moreover provide evidence that rewarded stimuli capture gaze (Hickey & van Zoest, 2013; Bucker, Belopolsky, & Theeuwes, 2015; Failing, Nissens, Pearson, Le Pelley, & Theeuwes, 2015). The fact that the oculomotor system is sensitive to valuation processes is not only evident in the fact where people look, but also when they move their eyes. Carpenter (1981) noted that two things are very striking about saccadic reaction times: They are surprisingly long and they are surprisingly variable. The shortest possible route from visual stimulation to motor response goes from the retina to the superior colliculus and from there to the brainstem where the saccade motor command is generated, and then send to the

extraocular muscles. The superior colliculus is a midbrain structure which is involved in the transformation of visual signals into motor commands. It is often described to contain both a map of visual space as well as a map for motor goals and is important for orienting movements (for review see Basso & May, 2017). Whereas this shortest neural pathway would take approximately 60 ms of signal transduction, saccade latencies are often more than three times as high. Carpenter (1981; see also Noorani & Carpenter, 2016) stated that this pathway through the superior colliculus would do a good job if all the oculomotor system had to do was to simply translate a visual signal into a motor response. Yet, these neurons in the superior colliculus would only know where a target is but not what it is. Determining the identity of a target could only be achieved in higher cortical areas of the oculomotor network. These cortical areas mostly have inhibitory connections to the superior colliculus and would have to prevent the superior colliculus from responding too early until a better analysis of what to look is carried out. Carpenter (1981) thus remarked that saccade latencies are the result of oculomotor procrastination and that most of the reaction time is decision time used to arrive at a more sophisticated decision of *what* to look at. Therefore, saccade eye movements are not only a decision in space but also a decision in time with saccade latencies being informative about the underlying decision process.

## 2.1 Saccade eye movements and motivational value

Anyone making a decision can maximize his or her outcome by considering the expected gain of an option as well as the probability to obtain this gain. This common ground of many decision making theories has been applied to visual saccadic decision making and saccade eye movements have become a favored model to study decision making in general (Platt & Glimcher, 1999; Glimcher, 2003; Kable & Glimcher, 2009). This is not only because saccades are executed so frequently but also because the oculomotor system is sensitive to valuation processes which becomes evident in the fact that reward influences several aspects of saccade eye movements. It can bias where people look, when they move their eye, but also the saccade motor program itself which is reflected in reward-induced effects on saccade kinematics. For example, saccades to rewarded targets have higher peak-velocities, both in monkeys (Takikawa, Kawagoe, Itoh,

Nakahara, & Hikosaka, 2002; Chen, Hung, Quinet, & Kosek, 2013) and humans (Chen, Chen, Zhou, & Mustain, 2014).

A prominent finding in human and animal decision making is temporal discounting, that is, the preference of sooner smaller rewards over higher rewards at a later point in time (Rodriguez & Logue, 1988). A recent study asked participants to decide between an immediate smaller reward or a delayed reward with higher magnitude (Reppert, Lempert, Glimcher, & Shadmehr, 2015). During the decision phase the two options were displayed left and right from the central fixation cross and participants were free to saccade back and forth between them. Participants had to press a button to indicate which option they would prefer. After the decision, the two options would still be displayed for the remaining decision phase. Peak-velocities were generally higher before participants made a decision. However, shortly before participants arrived at a decision, peak-velocities were also higher for saccades to the preferred compared to the non-preferred option. This difference in peak-velocities scaled with the difference in subjective value between the two options, suggesting that the subjective value that the brains assigns to an object is reflected in the peak-velocity towards that option and thus in the saccade kinematics (Reppert et al., 2015).

Information about value also influences where people look (Schütz, Trommershäuser, & Gegenfurtner, 2012; Theeuwes & Belopolsky, 2012; Ackermann & Landy, 2013; Bucker et al., 2015). Targets which have previously been associated with a high reward capture gaze more than low reward targets when they are flashed in a search array as distractors (Theeuwes & Belopolsky, 2012). When two targets are in close proximity, the saccade typically lands in-between the two (Coren & Hoenig, 1972; Findlay, 1982). Using this so-called global-effect, it has been shown that when participants are instructed to saccade to one of the two targets, saccade endpoints are more biased towards the other one when this other target signaled that in this trial a high compared to a low reward can be obtained (Bucker et al., 2015). A study which contrasted salience and motivational value showed that both can bias saccade endpoints, but that more weight is given to value information for saccades with longer latencies (Schütz et al., 2012). The authors concluded that the relative weighting of salience and value is probably reflected by the relative neural activity of a salience and a value priority map. This notion is consistent with neurophysiological findings that suggest that higher cortical areas, like the lateral intraparietal area (LIP), combine bottom-up and top-down information (Bisley & Goldberg, 2010).

Saccades to rewarded compared to unrewarded targets are initiated earlier, both in monkeys (Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Watanabe, Lauwereyns, & Hikosaka, 2003) and in humans (Dunne, Ellison, & Smith, 2015). Shorter latencies to rewarded targets are preceded by a higher discharge rate of neurons in parts of the basal ganglia, for example the caudate nucleus (Kawagoe, Takikawa, & Hikosaka, 1998; Itoh et al., 2003; Watanabe et al., 2003) and substantia nigra (Sato & Hikosaka, 2002), as well as in the deeper layers of superior colliculus which receive input from the basal ganglia and cortical regions (Ikeda & Hikosaka, 2003). Saccade latencies are not only reduced by the presence of reward but can also be delayed by the presence of a penalty (Schütz et al., 2012). Because reward and penalties are both motivational salient but differ with regard to their motivational value, this suggests that saccade latencies might not be related to the motivational salience but to the expected motivational value of a target. Milstein and Dorris (2007) directly tested whether saccade preparation is influenced by expected motivational value. They systematically investigated the influence of different reward magnitudes and probabilities on saccade latencies. Their results suggest that the oculomotor system is not only sensitive to reward in general but also sensitive to different levels of reward magnitude and the probability to obtain this reward. Although saccade latencies were affected by both factors, latencies showed a clear negative correlation with the multiplicative combination of the two – which is expected value (Milstein & Dorris, 2007, 2011). From that, Milstein and Dorris (2007) concluded that a representation of expected motivational value is used for the preparedness of saccades.

Other studies tried to shed further light on the mechanisms how reward influences oculomotor behavior. Based on animal models which suggest that the role of dopamine is to mediate the incentive salience of a reward (Berridge & Robinson, 1998), Hickey and van Zoest (2012, 2013) tested the hypothesis that reward can affect the salience of a stimulus. Their participants had to do vertical saccades to an either green or red target. A distractor of the respective other color was displayed slightly to the left or to the right of the direct connection between fixation cross and target (Hickey & van Zoest, 2012). In an experimental setup like this, saccade trajectories are influenced by the presence of a distractor (van der Stigchel, 2010): Short latency saccades curve towards the distractor, whereas long latency saccades curve away from it. The distractors salience is supposed to be reflected in the time course of this deviation. In the experiment by Hickey and van Zoest (2012), participants randomly received either a high or a low reward for a correct saccade to the target and were instructed to ignore the distractor. Target and distractor could change colors

from one trial to the other or they could stay the same. Thus, in trials in with a color change, the distractor now has the same color as the previously high or low reward target. When the distractor signaled a high reward compared to a low reward, then short latency saccades showed stronger curvature towards the distractor whereas long latency saccades showed stronger curvature away – the same pattern as would have been expected when increasing the distractors saliency. From that the authors concluded that reward can affect the perceptual salience of a target. The time course observed by Hickey and van Zoest (2012) shows high similarities with the time course observed by Schütz, Trommershäuser and Gegenfurtner (2012), both with respect to saccade endpoints as well as curvature away from the penalized zone. This might suggest that findings from both studies might be explained by similar mechanisms, for example the combination of a saliency map with a value priority map.

A recent study suggested that motivation by reward operates outside the speed-accuracy trade-off (Manohar et al., 2015). The speed-accuracy trade-off is an established law in motor control describing the phenomenon that faster actions become less precise. Motivation by reward however, can decrease response times and increase response accuracy at the same time (e.g. Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002). To explain these seemingly controversial findings, Manohar and colleagues (2015) suggested a "cost of control". While the internal noise in the motor system usually depends on the strength of the motor command (Harris & Wolpert, 1998), there might be an additional cost to attenuate noise by a certain amount because it may require more neuronal resources and energy to reduce noise (Manohar et al., 2015). Motivation by reward might thus be helpful in acquiring rewards earlier without diminishing accuracy.

In sum, there is ample evidence that the oculomotor system is sensitive to reward, reflected in the when and where of an eye movement as well as its kinematics. However, it might be argued that eye movements usually do not provide reward, but they are used to sample the environment and thus provide information for visual perception.

## 2.2 Saccade eye movements and their perceptual consequences

Saccade eye movements shift the fovea towards objects and regions of interest to allow high-acuity processing. Therefore, every saccade has direct consequences for visual perception and

the oculomotor system is sensitive to these consequences. The most direct consequence of a saccade eye movement is that the whole visual image is shifted across the retina. During the saccade itself visual information is suppressed (Zuber & Stark, 1966; Burr, Morrone, & Ross, 1994) and as a consequence, new visual information is mainly acquired during fixation. Thus, every new fixation differs with regard to the location of an object on the retina. Is the visual system able to integrate information from different fixations? An early study suggested this to be the case (Jonides, Irwin, & Yantis, 1982). Participants had to indicate a missing dot in a five-by-five dot matrix. The remaining 24 dots were not all showed simultaneously but in two frames, one frame with the first 12 dots was shown in the periphery, whereas the second frame with the remaining 12 dots was shown around the time of the expected saccade onset and was thus visible after saccade offset with foveal vision. Participants would only be able to indicate the missing dot if they were able to perceptually fuse the two frames and the results suggested this to the case. However, one year later, four studies were published that contradicted the notion that information is integrated across saccades (Bridgeman & Mayer, 1983; Irwin, Yantis, & Jonides, 1983; O'Regan & Lévy-Schoen, 1983; Rayner & Pollatsek, 1983) and revealed that the earlier results obtained by Jonides, Irwin and Yantis (1982) were caused by phosphor persistence on the screen (Irwin et al., 1983).

Ever since it has been a matter of debate whether the visual system is able to integrate information across saccades or not. Whereas some authors even claimed that perception starts anew with each fixation (Irwin, 1991; Bridgeman, van der Heijden, & Velichkovsky, 1994), other studies favored the view that information can be integrated across saccades (Melcher & Morrone, 2003; Demeyer, De Graef, Wagemans, & Verfaillie, 2009, 2010). Seeing the target not only after but also before a saccade improves target recognition (Demeyer et al., 2009), and biases post-saccadic perception in the direction of the pre-saccadic stimulus value when the to be judged feature varies on a continuous dimension (Demeyer et al., 2010). Furthermore, this pre-saccadic bias increases with decreasing uncertainty of the pre-saccadic display (Oostwoud Wijdenes, Marshall, & Bays, 2015). Whereas these studies nicely show that pre-saccadic information can bias perception and thus suggest that integration occurs, they do not provide conclusive evidence that pre- and post-saccadic information are actually integrated, because they cannot ultimately exclude other processes like cue switching (see 2.4.2 for further discussion). Thus, currently there are different viewpoints in the literature whether the perceptual system is able to continuously gather information about the same object despite making eye movements.

The perceptual consequences of an eye movement also strongly depend on the information that an observer seeks to obtain. In everyday activities like making a cup of tea (Land, Mennie, & Rusted, 1999) or preparing a sandwich (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003), the spatial and temporal distribution of gaze is tightly coupled to the task that is carried out. The presence of a task also has strong influences on the oculomotor system in more controlled laboratory settings. For example, saccade latencies are reduced by about 40 ms (Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Guyader, Malsert, & Marendaz, 2010; Bieg, Bresciani, Bülthoff, & Chuang, 2012) and peak-velocities are increased (Montagnini & Chelazzi, 2005; Bieg et al., 2012) when participants have to perform a perceptual discrimination task at the saccade target compared to when they are instructed to quickly look at a target upon appearance without the further requirement to process it. This perceptual task effect is independent of whether participants receive feedback about the outcome of the task or not (Bieg et al., 2012) and is spatially specific and thus does not depend on a generally increased arousal (Montagnini & Chelazzi, 2005). A perceptual task is also sufficient to elicit saccadic adaptation (Schütz, Kerzel, & Souto, 2014; Schütz & Souto, 2015): When participants make horizontal saccades to a horizontally stretched array of characters, then the average saccade endpoint is located between the array center and the end which is closer to initial fixation. However, depending on which of the characters is associated with a perceptual task, both forward adaptation (increasing amplitudes) and backward adaptation (decreasing amplitudes) can occur (Schütz et al., 2014), likely caused by target selection within the array (Schütz & Souto, 2015).

Another direct perceptual consequence of a saccade is high-acuity vision of the saccade target. Collins (2012) showed that saccade latencies are increased in blocks in which the foveal vision of the target was prevented by extinguishing targets during saccades. She concluded that foveation facilitates behavior and that the expected sensory consequence of a saccade can be seen as a reward for the oculomotor system (Collins, 2012). Moreover, saccades are also sensitive to the image content which is foveated: Saccades have higher peak-velocities and shorter durations when participants expect to see a face after the saccade compared to when they expect to see scrambled noise (Xu-Wilson, Zee, & Shadmehr, 2009). Image content also influences saccadic adaptation (Meermeier, Gremmler, & Lappe, 2016, 2017). The typical stimulus to elicit saccadic adaptation is a dot which changes its position during the saccade and thereby induces an error on the retina between the fovea and the dots projection on the retina (McLaughlin, 1967). Over the course of

many trials, the oculomotor system adjusts its amplitude so that the saccade lands closer to the post-saccadic target location and thus reduces the retinal error. Adaptation is stronger when the target is the image of a human compared to scrambled noise (Meermeier et al., 2016) and it is stronger when a new human image is displayed every trial compared to repetition of the same image (Meermeier et al., 2017). This suggests that it may not only be rewarding for the oculomotor system to see something compared to nothing (Collins, 2012), but that the visual system assigns an intrinsic value to the information which can be acquired at the saccade target (Xu-Wilson et al., 2009).

## 2.3 Saccade eye movements and optimal information sampling

In recent years the viewpoint emerged that eye movements serve the purpose to gather information by reducing uncertainty about the external world (Tatler, Hayhoe, Land, & Ballard, 2011; Gottlieb, 2012; Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014). Evidence for this notion comes from studies investigating natural behavior (Sullivan, Johnson, Rothkopf, Ballard, & Hayhoe, 2012; Tong, Zohar, & Hayhoe, 2017) and from studies employing computational models that aim to reveal whether eye movements support perception optimally given the sensitivity across the retina (e.g. Najemnik & Geisler, 2005).

Many tasks we wish to perform often require several independent subtasks. For example, making a cup of tea requires to move the kettle to the sink, fill it with water, move it back, boil it, put tea in a mug and then add the boiling water. All these different subtasks in general require visual information and can be modelled as independent modules (Sprague, Ballard, & Robinson, 2007) and if the models state is not updated, uncertainty about the state grows. In the example of making tea, we would have to look at the mug while filling it with water in order to be certain that we do not spill hot water because of an overflowed mug. In line with this idea, participants in a simulated driving task more often fixated on a speedometer when it had higher uncertainty but only if it was relevant for the overall task (Sullivan et al., 2012). Similarly, in a walking task, participants looked more at obstacles when they had to avoid them, thus when they were task-relevant and the number of fixations increased with the uncertainty associated with the obstacles' location (Tong et al., 2017).

To estimate whether participants choose their eye movements in order to maximize all the information available, many computational models employ the participants sensitivity across the retina (Najemnik & Geisler, 2005, 2008; Renninger et al., 2007; Morvan & Maloney, 2012; Peterson & Eckstein, 2012; Ackermann & Landy, 2013). Morvan and Maloney (2012) investigated whether participants choose their saccade endpoints in order to maximize the probability of identifying targets given the constraints of the retina. Participants had to discriminate whether a white dot which could appear in one three horizontally arranged patches was either in the upper or lower half of the patch. The initial fixation position was vertically above the three patches and varied along the horizontal dimension. Upon saccade offset, the white dot could appear in either the left or the right patch with equal probability, but never in the center. Critically, the authors moreover varied the distance between the patches. When the patches were close together, the optimal strategy would have been to always saccade to the center patch, because the patches at both sides were still close enough so that the task could be solved with peripheral vision. When participants decided to look at a side patch, they would not be able to perform the task if the dot appeared at the other side. If, however, the patches were far apart, then participants would not be able to perform the task based on peripheral vision and would not benefit from a saccade to the center patch. Thus, the optimal fixation strategy should depend on the patch distance. Because the authors measured the sensitivity across the retina for every participant, they were able to predict the critical patch distance where participants should optimally switch from a central to as side-strategy. Results showed that participants did not adjust their strategy according to the patch separation, suggesting that human eye movement behavior was far from optimal in this task (Morvan & Maloney, 2012). Similar results have been obtained by Renninger, Verghese and Coughlan (2007). Their findings also suggest that fixation locations were selected in order to reduce the local uncertainty at the selected position, but not globally across a wider region of the visual field.

Opposite findings have been obtained by Najemnik and Geisler (2005). In their study, participants had to find a sine-wave grating in a noisy background. The target contrast as well as the background noise were manipulated. Based on each individuals visibility map, the authors modelled the distribution of fixations. Their optimal search model had precise knowledge about the exact statistics of the scene as well as about its own visual system. Moreover, the model assumed that information was optimally integrated across saccades. This optimal search model

showed a strong agreement with the performance of human participants with respect to the number of fixations required to find the target. In contrast to the findings by Morvan and Maloney (2012) as well as Renninger and colleagues (2007), the work by Najemnik and Geisler (2005) suggests that the eye movements support perception optimally and that the visual system has an inbuilt representation of its own visibility across the retina and can make use of this representation for eye movement control. Moreover, it might suggest that humans are indeed able to integrate information from multiple fixations, although this topic is a matter of debate (see 2.2).

## 2.4 Aims and experimental approaches

The aim of this dissertation "*Eye movements and the maximization of value*" was to understand how valuation processes affect the control of saccade eye movements as well perception across saccades. Study I examined whether a representation of informational value is used for the preparation of saccades and whether this can explain the findings of earlier saccades to targets associated with a perceptual task. In Study II, we investigated whether the visual system maximizes all the information available across a saccade by integrating pre- and post-saccadic information according to their relative reliabilities. Study III tested whether the influence of motivational value on saccade preparation can only be found contexts in which people are additionally able to choose.

### 2.4.1 Study I: Saccade latencies and informational value

Study I examined whether a representation of informational value is used for saccade preparation and whether this might be able to explain why saccade latencies are reduced when the information acquired at the saccade target is task-relevant. Many previous studies have reported effects of motivational value on saccade eye movements (Takikawa et al., 2002; Chen et al., 2013; Dunne et al., 2015; Manohar et al., 2015). For example, Milstein and Dorris (2007) showed that saccade latencies are negatively correlated with expected motivational value, the combination of reward magnitude and probability. From that Milstein and Dorris (2007) concluded that a representation of expected motivational value is used for the preparedness of saccades. However,

it can be argued that receiving a monetary reward is an artificial scenario, because eye movements are usually not providing reward, but they are providing information. For every saccade target, the gain in information depends on the foveal target discriminability after the saccade relative to the pre-saccadic peripheral discriminability, or in simple terms, how well you can see something after shifting your gaze to it compared to how well you could see it beforehand. Is the oculomotor system also sensitive to the gain in information as it is to the gain in reward?

In order to compute the gain in information the visual system needs a representation of its own visibility across the visual field. Indirect evidence that the visual system knows about its own capabilities comes from optimal statistical models of eye movement planning (Najemnik & Geisler, 2005, 2008; Peterson & Eckstein, 2012). These models have an inbuilt assumption that the visual system has a representation of sensitivity across the retina and model predictions show a high similarity with human performance. However, this evidence is only correlational, because none of the abovementioned studies has explicitly tested whether expected informational value is used for saccade preparation.

Saccades are not only sensitive the reward magnitude but also to reward probability (Milstein & Dorris, 2007, 2011). An indication that the oculomotor system is not only sensitive to the probability of obtaining a reward but also to the probability of obtaining information, is the perceptual task effect: Saccades are initiated earlier by approximately 40 ms (Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Guyader et al., 2010; Bieg et al., 2012) and with higher peak-velocities (Montagnini & Chelazzi, 2005; Bieg et al., 2012) when the information which is gathered at the saccade target is relevant for a perceptual task compared to when participants are instructed to foveate the saccade target as quickly as possible without further processing. This difference between task-related and pure target-elicited saccades corresponds to task-probability values of 1 and 0. Indeed, the latency benefit caused by a perceptual task has a similar magnitude compared to the latency difference between targets with the least and highest expected motivational value in the study by Milstein and Dorris (2007).

In this study, we defined informational value as the multiplicative combination of information gain and the probability that information is task-relevant. Information gain on the other hand was defined as the ratio between foveal and peripheral discriminability. Usually, a saccades' gain in information only depends on the foveal and the peripheral sensitivity and does not change drastically over time. Therefore, to manipulate the information gain in our study, we used a gaze-

contingent display: While participants saccaded to targets appearing in the periphery, we exchanged the target during the saccade to independently manipulate the target shown in periphery and in the fovea. As vision is mostly suppressed during saccades (Zuber & Stark, 1966; Burr et al., 1994), exchanging the saccade target remains unnoticed to the participant. For our main experiment, we initially measured every participants' discrimination performance at both eccentricities, both in the periphery as well as in the fovea. From these measurements we derived contrast values that either correspond to below or above threshold performance for both eccentricities. This independent manipulation of the peripheral and foveal target allowed us, for example, to construct conditions in which participants would lose information by making an eye movement towards the target, because the saccade target was displayed above threshold in the periphery before the saccade and below threshold in the fovea after the saccade. If the oculomotor system is sensitive to informational value, then it should be able to adapt to changes in information gain and we would expect that a higher gain in information is associated with shorter latencies. Moreover, latencies should also decrease with increasing task-probability.

### 2.4.2 Study II: Optimal trans-saccadic integration

Study II investigated whether the visual system is able to integrate pre- and post-saccadic information according to their relative reliabilities and is thus able to maximize the visual information available across a saccade eye movement. Humans constantly move their eyes towards new objects of interest. Due to the inhomogeneous visual representation across the retina, peripheral vision usually selects objects as saccade targets, whereas foveal vision is used after the saccade to process objects at high resolution. As vision is mostly suppressed during saccades (Zuber & Stark, 1966; Burr et al., 1994), we have at least two pieces of information for every object we look at: pre-saccadic peripheral and post-saccadic foveal information. The question then arises, how the visual system deals with these two pieces of information? Does the foveal representation replace the peripheral one? Or are both integrated into a common trans-saccadic percept? And if they are, to which extent?

Although recent studies showed that pre-saccadic information can bias post-saccadic perception (Demeyer et al., 2010; Oostwoud Wijdenes et al., 2015) and thus challenge the view

that vision starts anew with each fixation (Irwin, 1991; Bridgeman et al., 1994), these studies cannot ultimately exclude that other processes than integration are involved. When it comes to the integration of information from different sensory modalities or the combination of different cues, maximum-likelihood estimation (MLE) has proved itself as the ideal solution to test whether two or more perceptual estimates are integrated into one (for review see Ernst & Bülthoff, 2004). Moreover, it can also specify the upper benchmark of integration and predict the optimal integrated percept. Here, *optimal* means that every estimate is weighted according to its relative reliability in order to minimize the uncertainty in the integrated percept. Let's consider the example that you see somebody knocking at a door. If you do so, you will have a visual estimate of where he or she knocked, because you saw where the hand touched the door. But you also have an auditory estimate, as you additionally heard the knocking sound. The auditory modality is worse in localizing events (Alais & Burr, 2004), so the auditory estimate is very likely associated with more uncertainty or one would say: it is less reliable. In this example, MLE makes two easy to test predictions that help to reveal whether your visual and auditory estimate are integrated: First, if both estimates are not identical but differ slightly with regard to their location judgment, then the integrated estimate will be somewhere in-between the two and it will be closer to the more reliable one, that is closer to the visual estimate. Second, the integrated estimate will be more reliable than each of the single estimates on their own. Thus, if you judge the location not only once but multiple times, your response will be less variable when you base your response on the integrated percept compared to just one modality.

This second prediction is even more important than the first one in order to show that information is integrated. Whereas the second prediction on the reliability can only be fulfilled if people integrate, the first prediction on the bias could theoretically also be explained by cue switching: If people base their judgment on one cue each trial, but alternate between the two cues across trials according to their relative reliability, then cue-switching would yield the same predictions as MLE integration with regard to the bias. Thus, all studies on trans-saccadic integration that reported biases but missed to report reliabilities at the same time (Demeyer et al., 2010; Oostwoud Wijdenes et al., 2015) cannot distinguish between integration and cue switching. In Experiment 1 and Experiment 2 we applied maximum-likelihood estimation to trans-saccadic integration. We measured peripheral weights (Experiment 1) and the reliability of trans-saccadic perception (Experiment 2) and compared these to MLE predictions which we deriverd from

separate measurements of pre-saccadic peripheral and post-saccadic foveal vision. In both experiments, we varied the reliability of the fovea by changing its contrast. If the visual system integrates information across saccades, we expected that peripheral information biases trans-saccadic perception and that this bias increases with decreasing foveal reliability. Most importantly however, the reliability of trans-saccadic perception should be higher than with either foveal or peripheral vision alone.

In Experiment 3, we outlined the time course of trans-saccadic perception using a classification images approach which is often also referred to as reverse correlation (for review see Murray, 2011). In a typical classification image experiment, stimuli are very little or not at all defined by the signal but mostly by a noise field. The noise field is either a spatial or a temporal distribution of independent Gaussian noise values. Participants perform a binary task, for example whether the target was present or absent, and trials are then divided according to the participants' responses. In case of a temporal noise field (i.e. noise values varying over time), the difference in the average noise values between the two response categories will reveal how much each time point contributed to the participants' response. Instead of averaging and subtracting noise values for both response categories, the two distributions of noise values can be told apart using an ROC analysis (Ludwig et al., 2014). The area under the ROC curve is then informative how much each point in time contributed to the overall percept. We expected that, consistent with Experiment 1, peripheral information would bias trans-saccadic perception and this bias would be stronger with a decreased foveal contrast. The exact pre-saccadic time course will help to reveal whether trans-saccadic perception shows similarities with pre-saccadic attention shifts or saccadic suppression. The former would predict a continuously increasing weight until saccade onset whereas the latter would predict a decrease in the peripheral bias right before the saccade.

### 2.4.3 Study III: Choices induce the effects of motivational value on saccade latencies

Study III investigated whether choices induce the effects of motivational value on saccade preparation in response to single rewarded targets. When making decisions between different prospects, humans can maximize their payoff by choosing the option with the highest expected value. In the literature, there are contradictory findings whether expected motivational value is also

used for movement preparation in order to minimize reaction times and receive rewards earlier. Some studies did find an influence of reward magnitude on saccade latencies (Milstein & Dorris, 2007, 2011), whereas others did not (Leon & Shadlen, 1999; Platt & Glimcher, 1999).

Milstein and Dorris (2007) rewarded participants for making saccade eye movements to one single target which either appeared left or right from fixation. They varied the reward magnitude between the two targets and the relative probability of the left and the right target to appear. Saccade latencies were affected by both factors, reward magnitude and probability, but showed a clear negative linear relationship with the multiplicative combination of the two, which is expected motivational value. Based on this finding, the authors concluded that a representation of expected motivational value is used for the preparation of motor responses like saccade eye movements. However, what is special about the experiments by Milstein and Dorris (2007, 2011), is that they recorded different trial-types, which were intended to answer different questions, interleaved in the same experiments. Among others, they recorded trials in which both targets were displayed and people could choose between the two targets in order to obtain the corresponding reward.

It is possible that the simultaneous recording of these different trial-types might have interacted in a way that gave rise to the linear relationship between expected value and saccade latencies. A potential cause for this might be inter-trial priming (for review see Failing & Theeuwes, 2017). Inter-trial priming can influence saccade eye movements, especially when a competition among several targets is involved (Bichot & Schall, 2002; Belopolsky & van der Stigchel, 2013).

Study III thus investigated whether the presence of choices causes the effects of motivational value on saccade preparation. To this end, we measured saccade latencies in response to rewarded single targets (single-trial) which appeared either right or left of fixation. Depending on the hemifield, targets were either associated with a high or a low reward. As an independent variable, we included trials in which both targets appeared (choice-trials). In choice-trials, participants could choose between the two in order to obtain either the high or the low reward. Across blocks, we manipulated the proportion of choice-trials which were randomly interleaved in one block. We expected that the effect of reward magnitude on single-trials would be modulated by the proportion of choice-trials.

# 3 Summaries

## 3.1 Study I: Saccade latencies and informational value

### Reference

Wolf, C., & Schütz, A.C. (2017). Earlier saccades to task-relevant targets irrespective of relative gain between peripheral and foveal information. *Journal of Vision*, *17*(6):21, 1-18. doi:10.1167/17.6.21

### Summary

Study I tested whether saccade preparation is not only modulated by motivational value (Milstein & Dorris, 2007) but also by informational value. We defined informational value as the multiplicative combination of information gain and the probability that information acquired at the saccade target will be task-relevant. Information gain was defined as post-saccadic foveal compared to the pre-saccadic peripheral discriminability of the saccade target, and thus corresponds to the amount of information which can be gained by saccade execution.

In a first experiment, we tested whether saccade latencies are influenced by information gain. Participants had to indicate whether the vertical orientation of a peripherally appearing plaid stimulus was tilted clockwise or counterclockwise (Figure 1A). We used a gaze-contingent display to independently manipulate the peripheral and foveal discriminability of the saccade target by changing the contrast ratio of the plaids vertical and horizontal component. Both, the peripheral and the foveal target could be displayed either above or below individual thresholds which had been determined beforehand. Thus, we had one condition, where participants would gain information by making an eye movement, one condition where participants would lose information and two conditions with equated discriminability, a difficult and an easy one. In each block we tested two of the conditions against each other, one assigned to each hemifield. All four experimental conditions always included a perceptual task. For every individual, we compared the average saccade latency across these four experimental conditions with a baseline condition

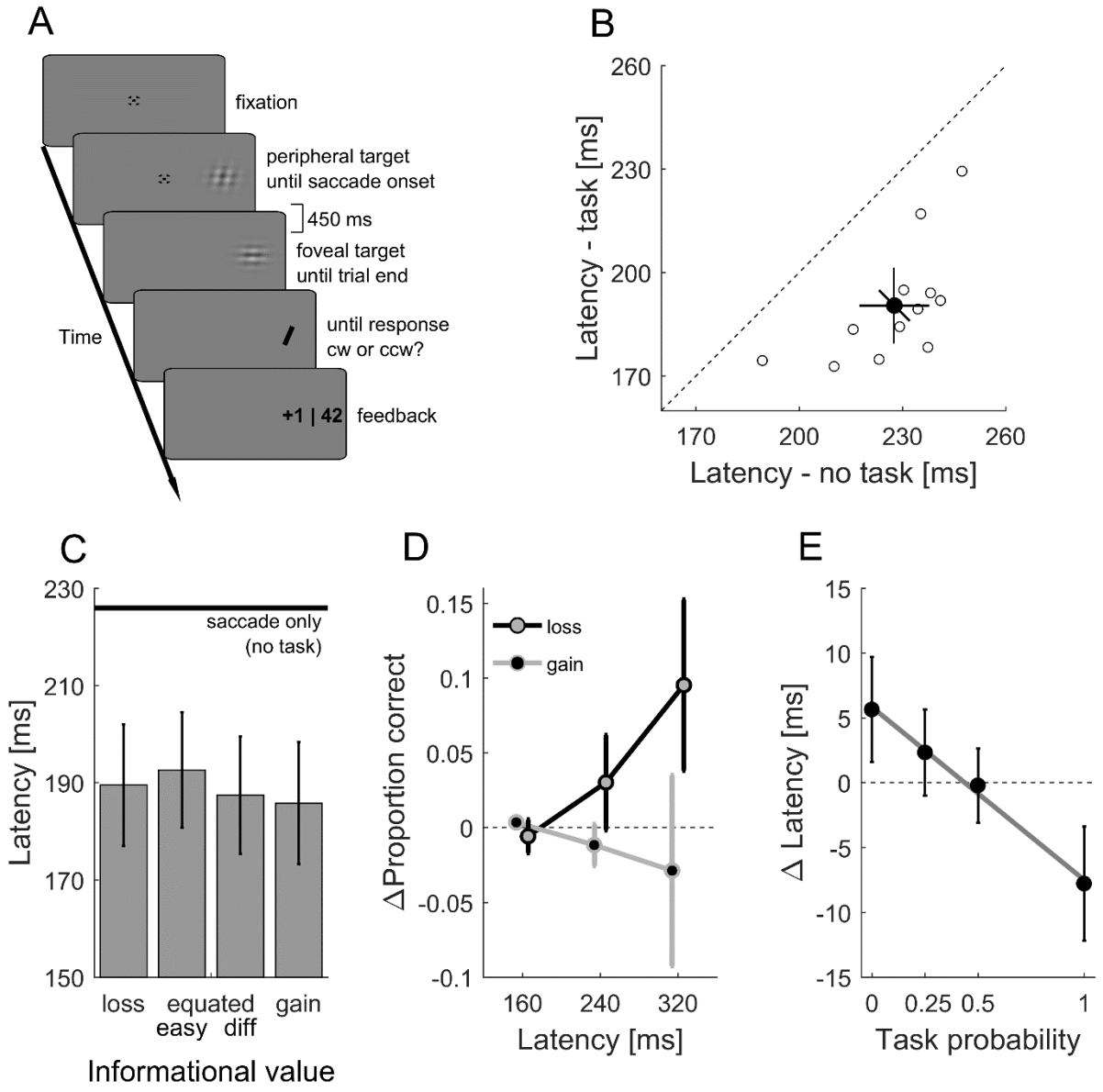


**Figure 1**. Study I. (**A**) Trial procedure for the perceptual saccade task in Experiment 1. A plaid appeared in the periphery and participants had to judge the orientation of the vertical component. The contrast of the vertical relative to the horizontal component was displayed either above or below individual peripheral thresholds. During the saccade, the relative contrast was adjusted to be either above or below individual foveal thresholds. (**B**) Effect of a perceptual task. Saccade latencies were reduced when participants had to do a perceptual task at the saccade target. (**C**). Saccade latencies with a perceptual task at hand did not differ no matter whether participants gain or lose information by making an eye movements. (**D**) In the loss condition, later saccades went along with a better performance, because participants could benefit longer from peripheral vision. (**E**) Latencies were modulated by the probability of a perceptual task at the saccade target. All error bars denote the 95%-confidence interval of between-participant variability.

without perceptual task, where participants were instructed to saccade to the appearing plaid stimulus as quickly as possible. In line with previous studies (Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Bieg et al., 2012), we found that saccade latencies are reduced when participants have to do a perceptual task at the saccade target (Figure 1B). However, we found no clear effect on the peak-velocity (data not shown). Latencies were not modulated by information gain, but were similar no matter whether participants lost or gained information by making an eye movement (Figure 1C). Previous studies have shown that saccade latencies can be adjusted to the requirements of a task (Madelain, Champrenaut, & Chauvin, 2007). However, here participants did not adjust their latencies, although performance increased with increasing latencies in the loss condition and performance decreased with increasing latencies in the gain condition (Figure 1D).

In Experiment 2, we tested whether saccade latencies are modulated by information gain when the stimulus is blanked after the saccade has landed. Blanking the saccade target is known to provide separate access to the pre-saccadic peripheral and post-saccadic foveal information and allows better comparison of the two (Deubel, Schneider, & Bridgeman, 1996). Thus, blanking might prevent that the peripheral and foveal image are integrated into one common percept. Adjusting latencies to the gain in information would only be possible when the visual system has separate access to the peripheral and foveal discriminability. But even with a 100 ms blank, latencies in the loss and gain condition did not differ.

In Experiment 3, we investigated whether latencies are modulated by the second factor which we considered to constitute informational value: task-probability. Participants completed four blocks which differed in the probability that participants would have to respond at the end of a trial. Probabilities were 0, 0.25, 0.5 and 1. After target offset, either the central fixation cross appeared and participants continued with the next trial or a vertical bar appeared at the target location in which case participants had to report the plaids' vertical orientation. Latencies decreased linearly with task-probability (Figure 1E), suggesting that saccade preparation can be influenced by the probability that information at the saccade target can become task-relevant.

In Experiment 4, we tested whether shorter latencies that go along with a perceptual task are caused by arousal. If the perceptual task effect is caused by arousal, then it should only depend on the task-probability within one block and should not be spatially selective. In Experiment 4, we compared latencies recorded within one block where participants would always have to do a perceptual task when the target appeared in one hemifield, but not if it appeared in the other one. We found shorter latencies for saccades to the hemifield that contained the perceptual task (Figure

2A). The magnitude of this effect was in the same range as in Experiment 1, suggesting that the perceptual task effect is spatially selective and cannot be caused by arousal.

In Experiment 5, we investigated whether the perceptual task effect also occurs for tasks in another modality. To this end we compared saccade latencies to plaid stimuli without a task and latencies when participants have to saccade to plaid and additionally perform an auditory pitch discrimination task. Latencies with and without auditory task did not differ significantly (Figure 2B). This indicates that the perceptual task effect only occurs for visual tasks at the saccade target.

Overall, our findings demonstrate that the relative gain between peripheral and foveal information is not used for saccade preparation. In contrast to that, saccade latencies were clearly influenced by task-relevance: Replicating earlier studies (Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Bieg et al., 2012), we found shorter latencies with a perceptual task at hand. The magnitude of this effect scaled with the probability that information acquired at the saccade target will be relevant for the task, suggesting the contribution of motivational factors. However, this facilitation cannot be caused by the general motivation to solve the task, because we found no facilitation with an auditory perceptual task. Thus, the facilitation due to a perceptual task seems to be caused by the motivation to foveate task-relevant visual information for further processing.

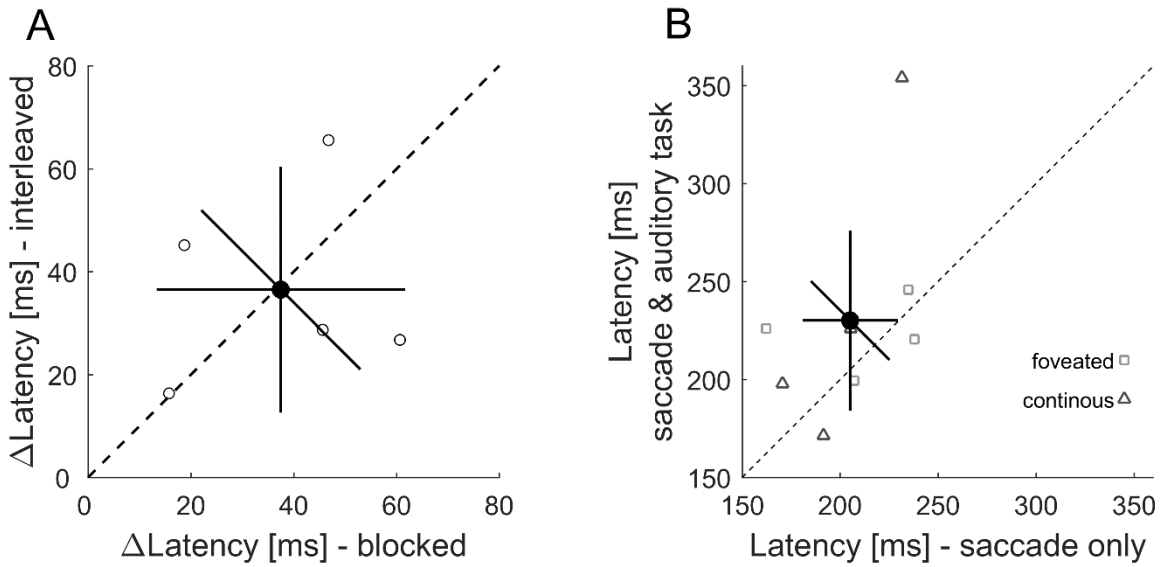


**Figure 2**. Study I. (**A**) Experiment 4. Latency differences between saccades without and with perceptual task when conditions were recorded in different blocks or interleaved in the same block. In the interleaved condition, saccade latencies to the hemifield containing a perceptual task were reduced. This argues against the hypothesis that global arousal causes the perceptual task effect. (**B**) Experiment 5. Latencies for saccades accompanied by an auditory perceptual task compared to saccade latencies without a perceptual task. Tones were played continuously as long as the plaid was displayed (triangle) or upon fovealization (square).

## 3.2 Study II: Optimal trans-saccadic integration

### Reference

Wolf, C., & Schütz, A.C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision*, *16*(16):1, 1-18. doi:10.1167/15.16.1

### Summary

Study II investigated whether humans integrate pre-saccadic peripheral and post-saccadic foveal information about an object in a statistically optimal manner. To this end, we measured the variability of both, the periphery and the fovea in an orientation discrimination task. From this, we predicted optimal trans-saccadic performance using maximum-likelihood integration. We then measured trans-saccadic perception and compared it to the benchmark of optimal integration. Maximum-likelihood integration makes two easy to test predictions: the first prediction is concerned with the optimal weight that should be given to each information and was tested in Experiment 1. The second prediction is concerned with the variability of the integrated percept and was tested in Experiment 2. In a third experiment, we explored the time-course of trans-saccadic information gathering using a reverse noise correlation approach.

Experiment 1 aimed to test the hypothesis that humans weigh peripheral and foveal information optimally. Participants had to saccade to a plaid stimulus appearing in the periphery and judge the orientation of its vertical component (Figure 3A). In integration trials, the plaid was visible before and after the saccade. However, it was rotated clockwise or counterclockwise by 2.5° during the saccade. This misalignment between peripheral and foveal orientation information allowed us to measure how much each of the two are weighted. A weight of zero would indicate no usage of this information whereas a weight of one would indicate usage of this information only. Moreover, we also manipulated the plaids' contrast: Whereas peripheral targets always had the same contrast, foveal targets either had a high contrast (same as periphery), a medium contrast or a low contrast. These three contrast values were chosen so that foveal performance was superior, similar or inferior to peripheral vision. This contrast manipulation allowed us to test whether the

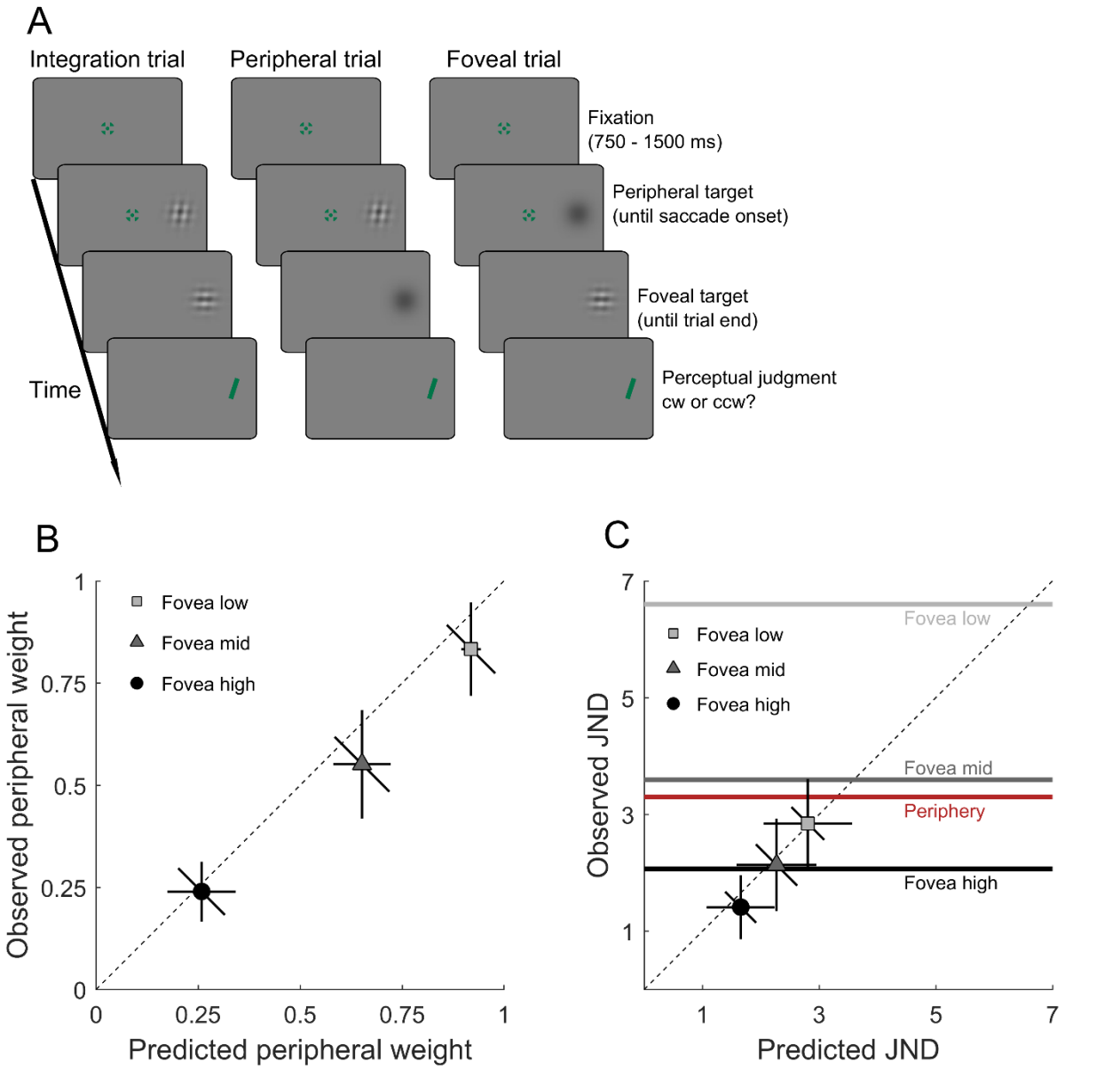


**Figure 3**. Study II. (**A**) Trial procedure in integration, peripheral and foveal trials. In all trials, participants had to saccade to a target in the periphery and judge the vertical component of a plaid stimulus. In peripheral trials, the plaid was only visible before the saccade and replaced by a blob afterwards. It was the other way round in foveal trials. In integration trials the plaid was visible throughout the trial but could be exchanged with regard to orientation and contrast during the saccade. For every observer, peripheral and foveal perception was used to predict perception in integration trials. (**B**) Observed against predicted peripheral weights. Observed weights on the identity line would indicate statistical optimal performance, whereas weights below (above) the identity line would indicate an overweighting of the fovea (periphery). (**C**) Observed against predicted just-noticeable differences (JND). JNDs on the identity line are statistically optimal. Integrated JNDs are significantly lower than with foveal or peripheral vision alone (horizontal lines). All error bars denote the 95%-confidence interval of between-participant variability.

weight given to the peripheral and the foveal estimate depends on the relative quality of the information. We hypothesized that the weight given to peripheral information increases with decreasing foveal contrast. In all three contrast conditions, the weight given to peripheral information was different from 0 (Figure 3B), suggesting that peripheral information was used in all conditions. Moreover, weights were also different from 1, indicating that also foveal information was used in all conditions. Most importantly however, peripheral weights increased with decreasing foveal contrast, indicating that peripheral information is weighted according to its relative quality.

To model optimal peripheral weights, we measured the variability of the peripheral and the foveal estimates separately. This was done in peripheral and in foveal trials (Figure 3A) using the same contrast(s) as in integration trials. In peripheral trials, the plaid was only visible in the periphery and replaced by a Gaussian blob during the saccade, whereas in foveal trials it was the other way round. Using maximum-likelihood estimation, we predicted optimal peripheral weights from these separate measurements (see original article for equations, Appendix, p.73). Predicted and observed peripheral weights coincided and did not differ significantly.

In Experiment 2, we tested the second prediction: If participants integrate across saccades, then the integrated percept should be more reliable (i.e. less variable) than each of its components. Experiment 2 was mostly identical to Experiment 1 except that there was no orientation misalignment between the peripheral and foveal target in integration trials. Variability, expressed as just-noticeable differences (JNDs), was lower in integration trials than with either peripheral or foveal vision alone (Figure 3C). We predicted JNDs in integration trials based on performance in peripheral and foveal trials. Observed and predicted values coincided closely.

In Experiment 3, we used a reverse-correlation technique to outline the exact time-course of information gathering around the time of saccades. Like in the previous experiments, participants had to judge the vertical orientation of a peripherally appearing plaid stimulus. However, the orientation was not constant but changed every 25 ms. Orientations were randomly drawn from a Gaussian distribution and participants were asked to saccade to the plaid and report whether the mean orientation was clockwise or counterclockwise. To analyse the data, noise values (orientations) were first aligned to saccade onset as well as offset. In a second step, we analysed on a millisecond basis how much noise values at this point in time contributed to the overall perceptual judgments. In line with the first experiment, this reverse-correlation technique revealed that

peripheral information from before the saccade is used and its contribution is higher when the foveal contrast was reduced (Figure 4). Moreover, information gathering decreased prior to saccade onset and was around chance performance during the saccade. Shortly before saccade offset information uptake started to increase again and was already elevated around saccade offset. In sum, the time course outlined here shares similarities with the sensitivity around the time of the saccade (Diamond, Ross, & Morrone, 2000; Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009). Limitations and implications of this experiment are discussed in more detail in the original article (Appendix, p. 84).

In sum, our results demonstrate that the visual system is able to integrate perceptual information across saccade eye movements in a near-optimal manner. The contribution of peripheral and foveal information is determined by the relative quality of peripheral and foveal vision. Vision across saccades thus does not correspond to single snapshots acquired from each fixation bur rather to a continuous, integrated stream of information.

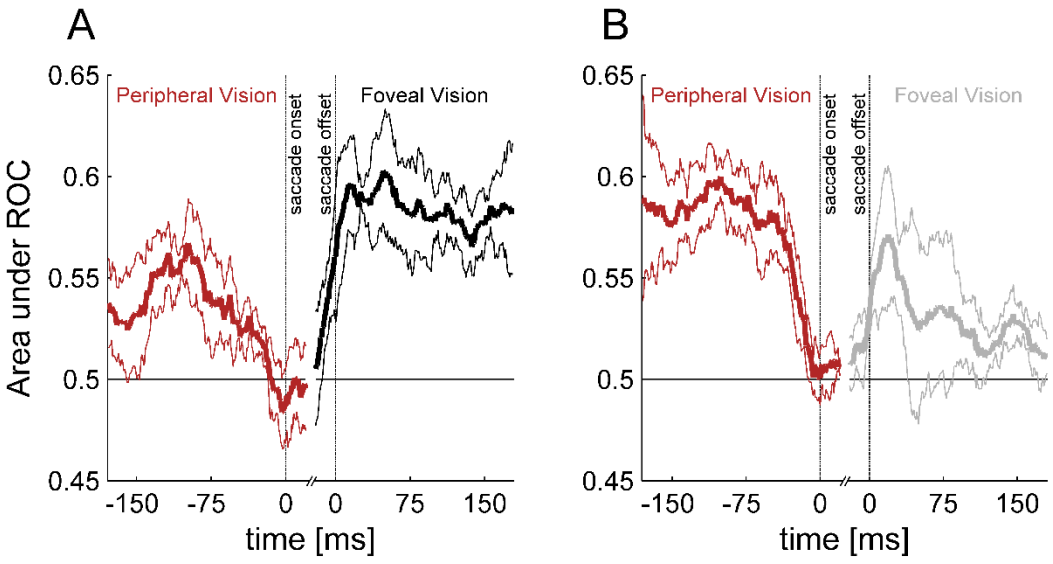


**Figure 4**. Study II, Experiment 3. Results from reverse correlation experiment for a (**A**) high and a (**B**) low foveal contrast. The area under the ROC curve (AUC) indicates the weighting of information for every time point. Whenever an AUC value is above 0.5, information at this point in time biased the trans-saccadic percept with higher AUC values indicating a stronger contribution. Thin lines correspond to the 95% confidence interval of between-participant variability.

## 3.3 Study III: Choices induce the effects of motivational value on saccade latencies

### Reference

Wolf, C., Heuer, A., Schubö, A., & Schütz, A.C. (2017). The necessity to choose causes the effects of reward on saccade preparation. *Scientific Reports*, *7*:16966.

### Summary

In Study III, we tested the hypothesis that choices induce the effects of expected motivational value on saccade preparation in response to single targets. To this end, we constructed an experiment with two different trial-types: single-trials and choice-trials (Figure 5A). In single-trials, one target appeared either left or right from fixation and participants received a reward when they saccaded to the target within 500 ms. Rewards were score points that were exchanged to a monetary reward at the end of the experiment. Targets on one side were always assigned a high, targets on the other one a low reward. In choice-trials, both targets appeared and participants could choose between the two in order to receive the corresponding reward. In all experiments choice-trials were only included as an independent variable, all analyses are based on single-trial latencies.

In Experiment 1, we tested the hypothesis that the presence of interleaved choice-trials modulates the influence of reward on saccade latencies in single-trials. We varied the difference in reward magnitude between the two hemifields, which could either be high (‘+1’ vs ‘+9’) or low (‘+4’ vs ‘+6’). Moreover, we varied the proportion of choice-trials which were randomly interleaved in one block (0%, 25%, 75%). Without interleaved choice-trials, we found no evidence for reward affecting saccade latencies (Figure 5B). When choice-trials were present however, latencies to the less rewarded target were delayed. This observation was more evident with a higher proportion of choice-trials and was not modulated by the reward difference between the hemifields.

Results from Experiment 1 could be explained in terms of choice-trials or in terms of saccade probability: Because participants almost always saccaded to the highly rewarded target in choice-trials, there was an increasing imbalance of saccades towards both hemifields with an

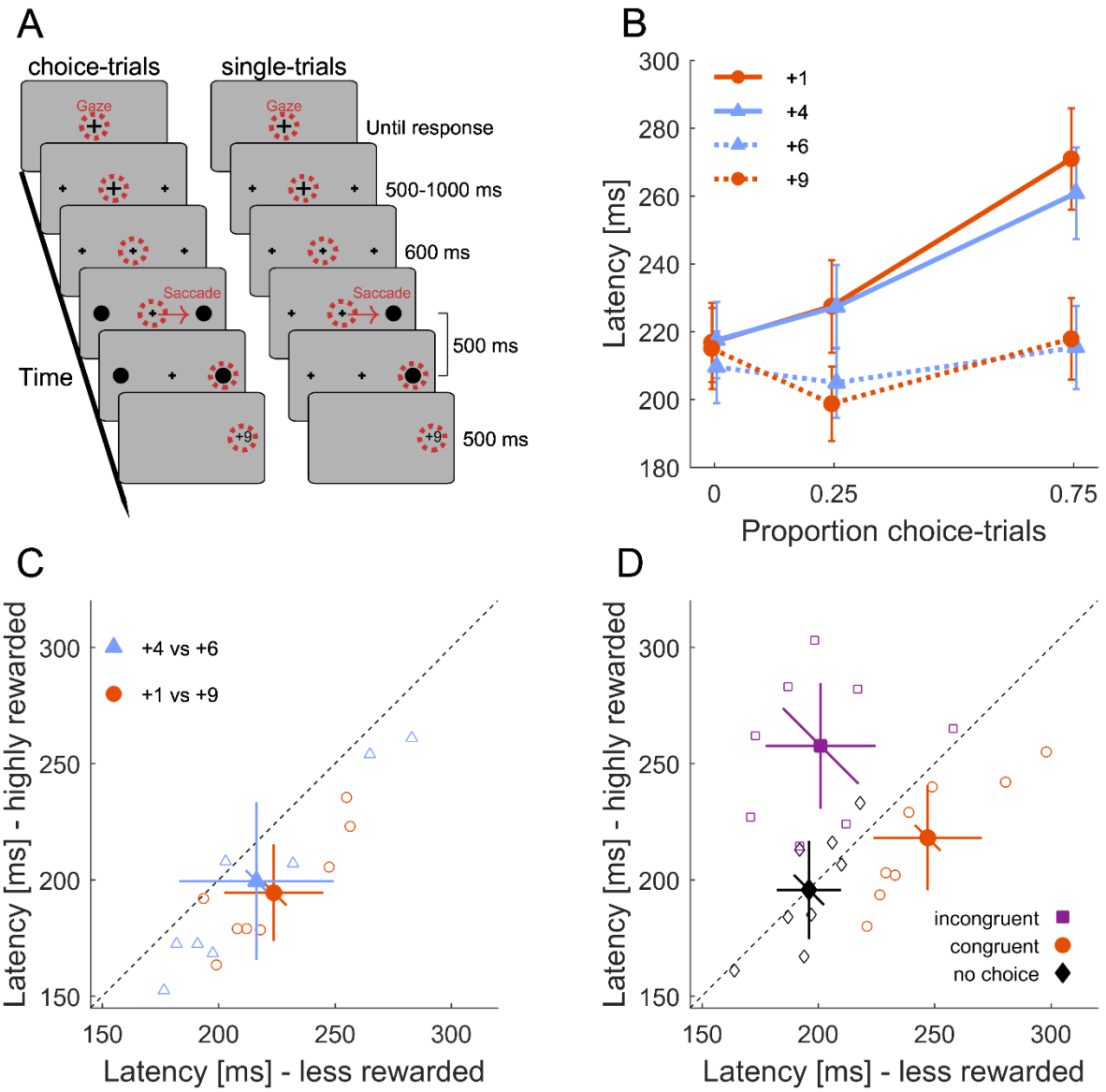


**Figure 5**. Study III. (**A**) Trial procedure in choice- and single-trials. In single-trials participants received a reward for saccading to one upcoming target. Depending on the hemifield, rewards were high or low. In choice-trials both targets appeared and participants could choose between the two to receive the corresponding reward. Only single-trials were analyzed, choice-trials were included as independent variable. (**B**) Experiment 1: Single-trial latencies as a function of the choice-trial proportion and the different levels of reward. Saccades to low versus high reward targets only differed when choices were interleaved. (**C**) Experiment 2: Latencies for the highly and the less rewarded target for the two reward differences when saccade frequency was matched for both hemifields (**D**) Experiment 3: Single-trial latencies for the highly compared to the less rewarded target when the choice-trial reward was incongruent (purple square), congruent (orange circle) or when choice-trials were absent (black diamond). All error bars denote the 95%-confidence interval of between-participant variability.

increasing number of choice-trials. To rule out this possible confound, we conducted Experiment 2. Here, we included 25% of choice-trials with 25% of single-trials to the highly and 50% of single-trials to the less rewarded side. Thus, in total, participants would saccade equally often to both hemifields if they always chose the highly rewarded target in choice-trials. Even without this imbalance in saccade frequency, we found the same difference between latencies to less and highly rewarded targets that were in a similar magnitude as in Experiment 1 (Figure 5C). This suggests that the effects obtained in Experiment 1 were due to the interleaved choices and not due to differences in saccade frequency.

The results from the first two experiments allow two interpretations: Either the presence of choices modulated the effect of single-trial reward or choices themselves caused the latency difference in single-trials. Experiment 3 aimed to differentiate between these two alternatives. To this end, we varied the reward congruency between choice- and single-trials. In the congruent condition, if the highly rewarded target was in the left hemifield in single-trials, it would also be in the left hemifield for choice-trials. In the incongruent condition, this relationship was reversed. If choice-trials would modulate the influence of single-trial reward, then single-trial latencies should be higher for the less rewarded single-trial, both in the congruent and incongruent condition. If however, choices cause the latency difference, then latencies in the incongruent condition should be higher for highly rewarded single-trials. The results of Experiment 3 clearly support the latter notion and provide clear evidence that choices caused latency delays in single-trials (Figure 5D).

To reveal why interleaved choices cause latency delays to single-targets, we reanalyzed the data from the Experiment 1 with respect to inter-trial effects. We compared latencies for single-trials preceded by a choice-trial with single-trials preceded by a single-trial. After a choice-trial, saccades to the less rewarded target were delayed (Figure 6A), suggesting that the non-chosen target is inhibited in choice-trials and this inhibition propagates to the next trial and influences the reactive saccades in single-trials. Thus, inter-trial priming is one factor which determines the influence of choices on single target responses.

In Experiment 4 and Experiment 5 we additionally tested the contribution of bottom-up and top-down influences. In Experiment 4 we manipulated choice-trial difficulty by varying the relative contrast of the two targets. In the difficult condition, the highly rewarded choice-trial target had a low contrast, whereas the less rewarded one had high contrast. It was the other way round for the easy condition. Choice-trial targets in the medium condition and all single-trial targets were displayed at an intermediate contrast. If participants inhibit the less rewarded target in choice-trials,

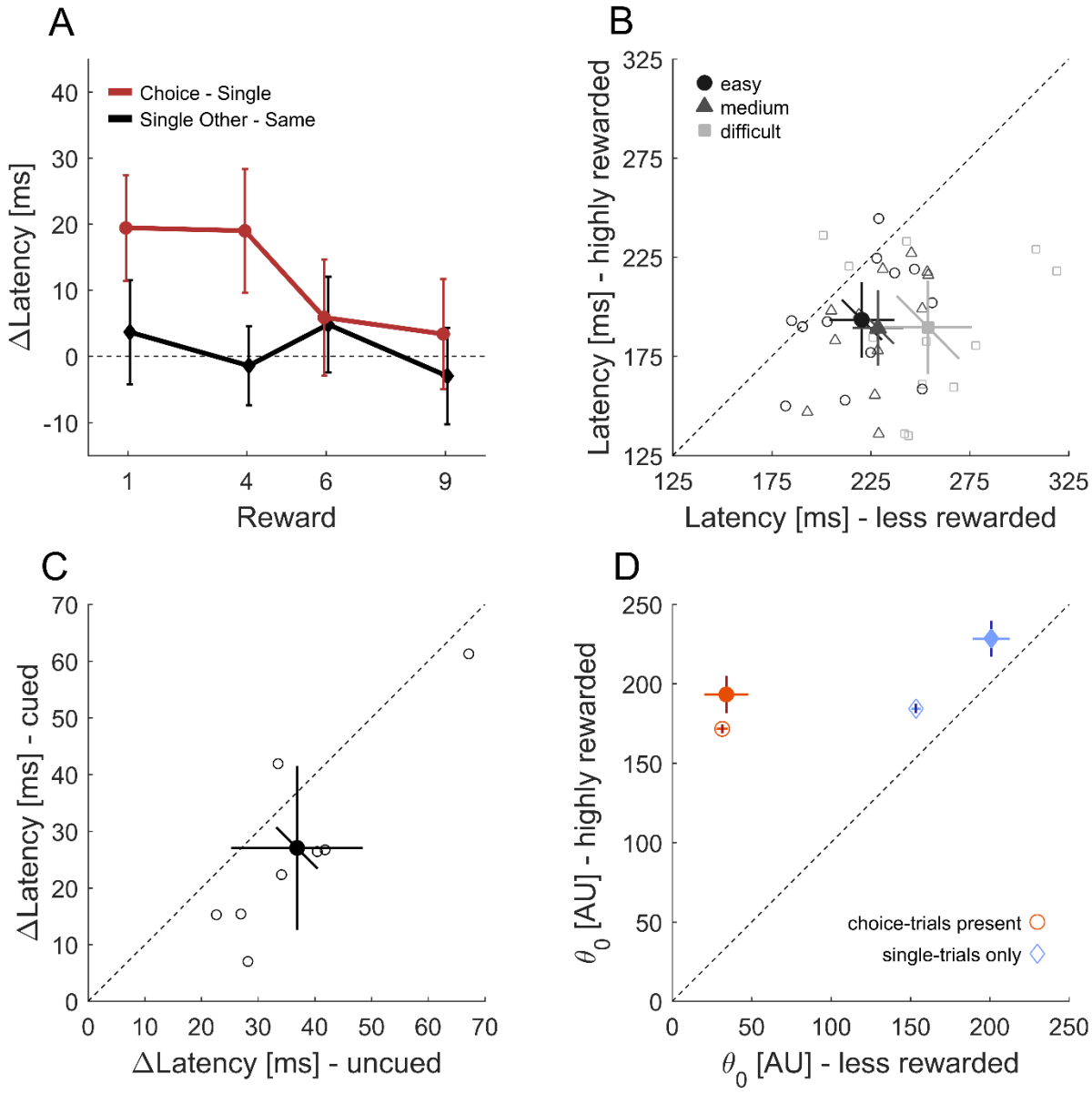


**Figure 6**. Study III. (**A**) Inter-trial effects. After choice-trials, latencies to the less rewarded and thus non-chosen target were delayed. This cannot be attributed to a change in saccade direction because no such delay occurred when single-trials were preceded by single-trials in the other direction. (**B**) Experiment 4: The effect of choice-trial difficulty. Single-trial latencies for the highly compared to the less rewarded target when choice-trials were easy (black circle), medium (grey triangle) or difficult (light grey square). Latency delays increased with difficulty (**C**) Experiment 5: Top-down effects. Single-trial latency difference between less and highly rewarded target when single-trials were cued compared to uncued. With a cue, latency differences were reduced. (**D**) Experiment 6: Results from the LATER model. Baseline levels, $\theta_O$, for the highly compared to the less rewarded target when choice-trials were absent (blue diamonds) or present (orange circles). Open and filled symbols distinguish the two participants. All error bars denote the 95%-confidence interval.

then the required inhibition should increase with difficulty and should thus lead to larger latency differences between less and highly rewarded targets in single-trials. In line with this, single-trial latencies to the less rewarded target increased with choice-trial difficulty (Figure 6B).

In Experiment 5, we tested the contribution of top-down influences. To this end, we cued half of the single-trials within one block. The cue was a "1" presented right above the central fixation cross during the preparatory period, thus before the target appeared. It signaled participants that the next trial will certainly be a single-trial. When single-trials were cued, the latency difference between less and highly rewarded targets was reduced compared to the uncued condition (Figure 6C). This indicates that participants could partially refrain from inhibiting the less rewarded target in preparation for a choice-trial and thus that there is also a top-down factor contributing to delayed saccades due to interleaved choices.

In a final experiment, we aimed to reveal likely neural mechanisms explaining the delay of saccades caused by interleaved choices. Therefore, we recorded and extended version of the experiment with two participants and fitted the LATER model to the data (Carpenter & Williams, 1995; Noorani & Carpenter, 2016). The LATER model is a rise-to-threshold model that can help to point out neural mechanism of decisions as well as simple responses, given the distribution of reaction times. The model assumes that for every motor response a response signal starts from a baseline level and rises with a constant rate until a threshold is reached. Although the rate of rise is constant within one trial, it varies between trials. The model thus has four free parameters: The baseline level, the threshold, the rate of rise and its variability. Since there is evidence that saccades are executed at a constant threshold (Hanes & Schall, 1996), we fixed the threshold parameter to a constant value and fitted the LATER model with the remaining three as free parameters. Results were best explained by changes in the baseline level. Whereas the baseline level for highly and less rewarded targets was in a similar range without choice-trials, the baseline level for responses to less rewarded targets was reduced when choices were interleaved (Figure 6D).

In total, our results suggest that there is no direct relationship between reward and saccade preparation in response to single targets. This relationship can only be observed when choices between two rewarded targets are interleaved. Choices delay saccades to the less rewarded target, because of inter-trial inhibition and the expectation of a choice-trial. Delays increase with the difficulty to make a reward-maximizing choice. Overall, this suggests that reward affects saccade preparation when the behavior is relevant for the outcome (as in choice-trials) but not for simple reactive saccades (as in single-trials).

# 4 General discussion

The present dissertation project examined how saccade preparation is influenced by informational (Study I) and motivational value (Study III) as well as the influence of informational value on trans-saccadic perception (Study II).

Study I investigated whether saccade latencies are influenced by the information in terms of target discriminability which can be gained by saccade execution and the probability that information will be task-relevant. Latencies were not affected by information gain and were thus not adjusted to maximize the information available. However, we replicated that the presence of a perceptual task reduced latencies and showed that this relationship is linearly modulated by the probability that information at the saccade target is task-relevant. Moreover, we could show that the perceptual task effect only occurs for visual and not for auditory tasks. Overall, we concluded that the perceptual task effect is caused by the motivation to foveate relevant visual information.

Based on the finding that saccade preparation is not adjusted to maximize the gain in information, we investigated in Study III whether the effects of motivational value on saccade preparation (Milstein & Dorris, 2007) are caused by interleaved choices between multiple rewarded targets. We found that reward affected saccade latencies in response to single targets only when choices were interleaved. Single-trial latencies to the less rewarded choice-trial target were delayed, irrespective of the reward in single-trials itself. This delay depended on the difficulty to choose the target with the higher reward and could be also be modulated by the expectation of the upcoming trial-type. After a choice, latencies in response to the less rewarded target were increased. Overall, this suggests that expected motivational is not used for saccade preparation per se. Instead, motivational value is used to maximize outcome by preferring one target over the other and this preference then propagates to reactive saccade and manifests itself in saccade latencies.

In Study II, we asked whether the visual system integrates information across saccade eye movement and in doing so maximizes all the information available. Specifically, we tested if the different resolutions of peripheral and foveal vision contribute to perception across saccade eye movements. For every individual observer, we separately measured discrimination performance in the fovea and in the periphery and used maximum-likelihood estimation to predict both, the optimal weight given to peripheral information as well as the variability which would results from optimal trans-saccadic integration. Human observers weighted peripheral information according to its

relative reliability and were closed to optimal peripheral weights. The variability of the trans-saccadic percept was lower than the variability of either peripheral or foveal vision alone and coincided with the predictions for optimal trans-saccadic perception. This is strong evidence that the human visual system is able to integrate information across saccades, that it maximizes the information available and thus that perception does not start anew with each fixation.

## 4.1 The influence of motivational and informational value on oculomotor control

The concept of a priority map is based on the saliency map concept (Itti & Koch, 2000) but combines bottom-up information about saliency with top-down information like expectations, behavioral goals and preferences (Fecteau & Munoz, 2006; Serences & Yantis, 2006; Ptak, 2012; Belopolsky, 2015). Effects of both, motivational value by reward (Milstein & Dorris, 2007; Schütz et al., 2012; Chelazzi et al., 2014) as well as task-relevance (Navalpakkam & Itti, 2005; Ipata, Gee, Bisley, & Goldberg, 2009), are said to be coded in such a priority map. Characteristics of a priority map have been reported for the intermediate layers of the superior colliculus (White & Munoz, 2011), the lateral intraparietal area (LIP; Gottlieb, Kusunoki, & Goldberg, 1998; Kusunoki, Gottlieb, & Goldberg, 2000; Gottlieb, 2007; Ipata et al., 2009; Bisley & Goldberg, 2010) and the frontal eye fields (FEF; Bichot & Schall, 2002; Thompson & Bichot, 2005).

Can the finding of earlier saccades to task-relevant targets (Study I) and increased latencies for saccades to less rewarded targets when choices are interleaved (Study III) be explained in terms of a priority map? The basic principle of a priority map is a topographic representation of space where salient or relevant (or both) locations receive a higher activity than less salient or relevant locations and many models assume a winner-takes-all mechanism where the location with the highest activation within the map will be attended next. Recently, it was suggested that both the spatial as well as the temporal aspects of the oculomotor decision are affected by the same mechanism (Tatler, Brockmole, & Carpenter, 2017). For example, physical salience does not only influence where we look but also when we move our eyes (Carpenter, 2004; Ludwig, Gilchrist, & McSorley, 2004). Thus, it could be possible that the priority maps' peak activation is related to the reaction time of a saccade. And in terms of a priority map, increasing the relevance of a target should qualitatively have the same influence on saccade latencies as increasing stimulus salience. Therefore, the observation that latencies decrease with the probability that information acquired at

the saccade target is task-relevant could be consistent with the idea that salience and relevance are coded together in a priority map which is used for attentional selection and eye movement control.

Can the results of Study III also be explained in terms of a priority map? At first sight, the finding that single-trial latencies were not affected by reward seems to contradict this notion. There are several explanations how this finding might relate to a priority map. First, it could be that the priority map is only sensitive whether reward is present or absent but does not discriminate between high and low rewards. Second, it might be that the relationship between the maximum of a single peak in the priority map and saccadic reaction time is non-linear. For example, if there is a highly salient and relevant object in the visual field, then latencies could not be further decreased by increasing the salience or relevance. A third explanation is that information about reward is only represented in the priority map when it is behaviorally relevant. In blocks with single-trials only, participants simply reacted to an upcoming stimulus and would always receive a reward. In blocks with interleaved choice-trials, participants can win or lose information depending on their saccade decision. That information about value was used can be seen from the fact that participants almost always chose the highly-reward target in choice-trials. It might be that the preference of one target over the other target is coded in a priority map, but not the level of reward per se.

In a recent review, Ptak (2012) defined five criteria to identify whether a neural site acts as a priority map. One of them was that the neural site should not only be activated by attention shifts or eye movements but should be effector independent. Recently, we replicated the findings of Study III using button-press responses instead of eye movements (Heuer, Wolf, Schütz, & Schubö, 2017). Like in Study III we looked at reaction times towards highly or less rewarded single-targets when choices were interleaved or not and the overall reaction time pattern was consistent with Study III. Moreover, the simultaneous recording of pre-stimulus oscillatory activity revealed an increase in lateralized alpha power in blocks with a high proportion of choice-trials. Modulations in alpha power are related to suppressed and facilitated processing of information. In line with that view, lateralized increases in alpha power correlated with reaction times towards the less rewarded target in single-trials, suggesting that the less rewarded target was suppressed in preparation for a choice-trial (Heuer et al., 2017). Moreover, a region which is said to contain a priority map, the frontal eye fields, are causally involved in the modulation of contralateral pre-stimulus alpha power (Marshall, O'Shea, Jensen, & Bergmann, 2015). In total, this suggests that the results of Study III can be described in terms of a priority map and that choices may modify the priority map via the expectation of an upcoming choice as well as inter-trial priming.

## 4.2 Inter-trial priming in oculomotor control

In Study III we found that a decision between two rewarded targets can give rise to a subsequent inhibition of the less rewarded and thus non-chosen target. Our study therefore also extends the growing body of literature reporting the effects of inter-trial priming on oculomotor control (Fecteau & Munoz, 2003; Failing & Theeuwes, 2017). However, many studies disagree whether inter-trial priming effects are facilitating or inhibitory. Facilitating inter-trial effects can occur when two saccades to the same target location occur in short succession (Dorris, Taylor, Klein, & Munoz, 1999). However, these facilitations have mostly been observed in the monkey and not in human observers (for review see Fecteau & Munoz, 2003). A well-studied example of an inhibitory inter-trial effect is *inhibition of return*, (IOR). When the eyes (or the focus of attention) move away from a location, then subsequent responses to stimuli appearing at that location are slowed down (Posner & Cohen, 1984; Klein, 2000). This phenomenon is supposed to reflect the preference of new compared to already attended stimuli or locations. The pattern of results which would have been predicted by inhibition of return is opposed to the pattern of results we obtained in our study. If our results would be caused by inhibition of return, then we should have observed delayed latencies to single targets which were chosen in a previous choice-trial. Thus, IOR would have predicted delayed latencies towards the highly rewarded and not towards the less rewarded single target after a choice. Moreover, IOR would have predicted inter-trial effects caused by preceding single-trials.

How then do the results of Study III and inhibition of return go together? One possible explanation could be derived from the studies by Tanaka and Shimojo (1996, 2000). They found that repetition of stimulus locations can lead to inhibition whereas repetition of stimulus features can lead to facilitation of return. Because two successive saccades to the highly rewarded target would not only involve a location repetition but also a repetition of the target feature, one possible explanation why we did not find inter-trial effects for highly rewarded target because inhibitory processes due to the identical location and facilitating processes due to the identical target feature cancel each other out. However, this scenario is unlikely given that in Experiment 4 of Study III choice-trial and single-trial targets differed with regard to a target feature (luminance) and despite that we did not observe inter-trial effects for highly rewarded targets in this experiment (data not reported). A more likely explanation are the different time courses in our study and studies reporting IOR. For example, Tanaka and Shimojo (1996) used response-stimulus intervals of up to

1800 ms with the strongest IOR for shorter intervals. In our study the time interval between a saccade and the onset of the stimulus in the next trial depended on how quickly participants started the next trial and thus lasted on average several seconds. Moreover, other visual events and eye movements during that period, like the onset of the central fixation cross and the accompanying gaze shift, might have overwritten the influence of the targeting saccade.

Whereas this might explain why we did not obtain inter-trial effects for highly rewarded targets, it still cannot explain why we found inter-trial effects for less rewarded targets after a choice-trial. These inter-trial effects might be caused by the fact that a saccade response to the less rewarded target during choice-trials is inhibited and this inhibition then propagates to the next trial. Evidence for this notion comes from a study investigating inter-trial effects in monkeys (Dorris et al., 1999): When monkeys had to suppress a saccade to a peripheral stimulus but had to saccade to a second peripheral stimulus which appeared later in time, then latencies were higher when the location of the first and the second stimuli matched compared to when they did not match. This suggests that the inhibition required to suppress an oculomotor response to a particular location can propagate to the next trial and influence the preparation of saccades to the same location. Similar evidence comes from paradigms switching anti-saccade and normal pro-saccade responses. In an anti-saccade task, participants have to inhibit a response to a peripherally appearing target and instead have to invert the saccade vector and shift their gaze into the opposite direction with the same amplitude. Pro-saccade latencies are increased when preceded by an anti-saccade (Cherkasova, Manoach, Intriligator, & Barton, 2002; Weiler & Heath, 2012). These switch costs are caused by response suppression and not by saccade vector inversion, because they also occur when a No-Go cue signaled to withhold a pro-saccade (Weiler, Mitchell, & Heath, 2014). These findings perfectly match with our interpretation that the suppressed response to the less rewarded target in single-trials causes a delay in a subsequent single-trial response to that location.

Which neural processes might give rise to the inter-trial effects observed in Study III? Any neural site that could serve as origin for the present inter-trial priming effects on saccade behavior should be involved in (i) saccade generation (specifically target selection), (ii) inhibiting other potential saccade targets, (iii) it should represent value and (iv) its activity should be modulated before and after an eye movement to influence the subsequent saccade. Both, the supplementary (SEF) as well as the frontal eye fields (FEF) fulfill these conditions. The FEF is typically known to be involved in saccade generation (Robinson & Fuchs, 1969), target selection (Schall & Hanes, 1993), but has also been shown to be involved in inter-trial priming of spatial position (Campana,

Cowey, Casco, Oudsen, & Walsh, 2007). The SEF on the other hand can influence saccade generation via connections to the FEF (Schall, Morel, & Kaas, 1993). Neurons in SEF anticipate saccade choices (Coe, Tomihara, Matsuzawa, & Hikosaka, 2002) and can have inhibitory effects on oculomotor behavior (Schlag-Rey, Amador, Sanchez, & Schlag, 1997). The same is true for the FEF: Preceding a saccade, conflicting movement vectors are inhibited within the two FEFs (Schlag, Dassonville, & Schlag-Rey, 1998) and stimulation in FEF excites the same but inhibits different movement vectors in the superior colliculus (Schlag-Rey, Schlag, & Dassonville, 1992). Moreover, pre-stimulus activity in FEF is associated with anti-saccade errors and negatively related with latencies of contralateral saccades (Everling & Munoz, 2000). Representations of value can be found in both sites (Roesch & Olson, 2003; So & Stuphorn, 2010). Most importantly, neurons in FEF and SEF respond not only before but also after saccades (Goldberg & Bruce, 1990; Stuphorn, Taylor, & Schall, 2000). Although the contribution of these neural sites remains speculative and the list is not exhaustive, both sites are likely candidates for the interface of inter-trial effects on oculomotor behavior. This is in line with the suggestion that both play an important role in evaluating preceding choices to optimize future behavior (Stuphorn et al., 2000; Stuphorn & Schall, 2006; Teichert, Yu, & Ferrera, 2014). A role of the FEF in inter-trial effects is also consistent with our finding that latency delays increased with the difficulty of a reward-maximizing decision in choice-trials (Study III, Experiment 4), because post-decisional activity in FEF scales with decision difficulty (Teichert et al., 2014).

## 4.3 The influence of informational value on trans-saccadic perception

In Study II we found that feature information is integrated near-optimally across saccades using orientation as task-relevant feature. Moreover, we varied the stimulus contrast in order to manipulate the relative reliability, thus the uncertainty, associated with the foveal stimulus. In line with previous and concurrent findings (Melcher, 2005; Ganmor, Landy, & Simoncelli, 2015) our findings suggests that information about contrast, which renders how well an object can be seen, is treated differently in trans-saccadic perception compared to other features like orientation or color. This might be related to the fact that how well an object can be seen differs drastically between peripheral and foveal vision and the purpose of any saccade is to bring objects from the periphery to the fovea. When the pre-saccadic peripheral and post-saccadic foveal target were

different with respect to orientation, the trans-saccadic percept yields a weighted average of the two information (Study II; Ganmor et al., 2015). Similar results that show that peripheral information can bias foveal perception have been obtained for form (Demeyer et al., 2010) and color (Wittenberg, Bremmer, & Wachtler, 2008; Oostwoud Wijdenes et al., 2015). A weighted average for contrast would be maladaptive for the visual system, because this would bias the high-resolution foveal image towards the low-resolution peripheral image and would thus downgrade perception. Quite to the opposite, the perceptual system seems to employ a strategy that maximizes visibility: By optimally weighing and integrating the peripheral and foveal image according to their visibility, it maximizes all the information available and can form a near-optimal percept.

But how can the visual system achieve this visual stability? A first prerequisite for visual stability would be that the visual system is able to distinguish external and self-induced motion on the retina. A neural principle that might account for this distinction is the efference copy (von Holst & Mittelstaedt, 1950), sometimes also referred to as corollary discharge. A pathway which codes this efference copy signal was identified from the superior colliculus (SC) via the mediodorsal thalamus (MD) to the frontal eye fields (Sommer & Wurtz, 2002, 2004, 2006). A recent study showed that this circuit is involved in visual perception (Cavanaugh, Berman, Joiner, & Wurtz, 2016). By inactivating the efference copy signal in MD, Cavanaugh et al. (2016) could decouple eye position from perception. Similar observations were found in human patients with lesions in MD (Ostendorf, Liebermann, & Ploner, 2010). Based on this neural circuit, the frontal eye fields were assigned a causal role in the perceptual stability despite making eye movements and predictions on the post-saccadic image were supposed to be extrapolated from the pre-saccadic image (Crapse & Sommer, 2008). This view is based on the finding that the FEF contains neurons which shift their receptive fields before an eye movement to the new post-saccadic location (Umeno & Goldberg, 1997). This phenomenon called *spatial remapping* has originally been described in LIP neurons (Duhamel, Colby, & Goldberg, 1992).

The notion that the visual system predicts the foveal image from the peripheral input is also supported by behavioral studies (Cox, Meier, Oertelt, & DiCarlo, 2005; Herwig & Schneider, 2014; Herwig, Weiß, & Schneider, 2015; Valsecchi & Gegenfurtner, 2016). Participants in an experiment by Herwig and Schneider (2014) first passed an acquisition phase where they could saccade back and forth between objects and where one object changed its spatial frequency during the saccade so that the foveal frequency was consistently higher or consistently lower than the peripheral one. In the subsequent test phase, participants had to saccade to a peripheral stimulus that disappeared

upon foveation and afterwards reported the spatial frequency. Perceived spatial frequencies were biased in the direction of the learned association between peripheral and foveal image (Herwig & Schneider, 2014). However, these effects were relatively small compared to the manipulation and it remains an open question whether feature prediction can account for trans-saccadic integration.

If the SC-MD-FEF pathway is responsible to spatially align objects despite making eye movements, this does not automatically imply that this pathway is also coding the uncertainty of the peripheral and foveal image and thus the weight that is given to each information. How the brain might represent this uncertainty can be revealed by studies on perceptual decision making: Human participants are able to choose the stimulus which is associated with less uncertainty, suggesting that the visual system has access to information about uncertainty (Barthelmé & Mamassian, 2009). In doing so, the visual system does not follow image cues to uncertainty, like contrast or eccentricity, but uncertainty is rather tightly coupled to performance (Barthelmé & Mamassian, 2010), indicating that there is no separate estimate of uncertainty in the visual system, but that uncertainty can directly be inferred from sensory estimates about particular objects or object features. This view is in line with probabilistic models of the brain, for example Bayesian or Maximum-Likelihood models, which model sensory estimates as probability distributions whose variability is equivalent to uncertainty (Ernst & Banks, 2002; Kersten, Mamassian, & Yuille, 2004). Newsome, Britten and Movshon (1989) compared the behavioral discrimination performance of a monkey with the discrimination performance of simultaneously recorded neurons in the middle temporal area (MT). Neurons in MT are sensitive to visual motion and have both, a preferred direction and a preferred velocity. The authors analyzed how well neurons could discriminate between their preferred and the opposite direction. Interestingly, discrimination performance of neurons was on average as reliable as the monkeys' behavioral performance with some neurons actually being better and other neurons being worse than behavior (Newsome et al., 1989). This work nicely shows that reliabilities of perceptual performance and neural activity are closely related and suggests that information about reliability might be coded in visual areas.

Thus, spatial remapping which has been observed in frontal and parietal neurons and which is probably based on an efference copy signal might be a potential candidate to explain how the visual system is able to relate the pre-saccadic and the post-saccadic image on the retina. Information about reliability of the pre-saccadic and post-saccadic information will likely be recruited from visual areas.

## 4.4 Future perspectives

Many of the findings revealed within this dissertation project inevitably led to new questions which would foster our understanding of the visual and oculomotor system. For example, near-optimal trans-saccadic integration, as reported in Study II, might only be found for the saccade target and integration might be less efficient for other regions in the visual field. Is object information from successive fixations integrated when participants do not saccade to an object like in Study II but when the object has already been foveated and participants saccade away? What happens when participants make more than just one eye movement but continuously shift their gaze to new locations: Does information from preceding fixations slowly decay over time and does it thus need to be updated by re-fixating an item? Answers to all of these questions, might be helpful to draw a complete picture of trans-saccadic perception.

Another source of potentially fruitful research questions arises from the idea of a priority map where information about saliency, current goals, value but also the previous selection history are combined (Belopolsky, 2015). If it is true that, for example, valuation and task-relevance modulate oculomotor control in the same way and share the same neural resources, then value effects and effects of task-relevance should interact with each other. Xu-Wilson, Zee and Shadmehr (2009) suggested that visual information might be intrinsically valuable, faces more than objects, and objects more than noise stimuli and they showed that this is reflected in eye movement kinematics. If coded in a common priority map, then the effects of valuation and task-relevance might have the same influence on oculomotor control. Then, a perceptual task could render invaluable stimuli, like gratings, relevant, whereas a perceptual task could not do much to stimuli that are intrinsically valuable per se, like face stimuli. When controlled for low level image information, an interaction of intrinsic visual value and task-relevance might reveal that both are coded in one priority map.

In a saliency map, the salience of an item or region is represented by the activity within the map and salient regions are represented by peak activity in the map. The relationship between stimulus salience and saccade latencies is probably not linear, and changes in contrast lead to larger changes in latencies for low contrast than for high contrast targets (e.g. Ludwig et al., 2004). Combining this observation with the above stated idea of a common priority map which combines salience, valuation and current goals, would imply a non-linear relationship between the peak-activity on the map and saccadic reaction times: The same increase in the priority map peak would

cause a stronger decrease in reaction times when the peak itself is small compared to when the peak itself is high. As a consequence, this predicts that valuation effects and effects of task-relevance can be increased by decreasing stimulus salience. As decreases in stimulus salience would also prolong saccade latencies in general, this possibility would have to be distinguished from the notion that value influences oculomotor control at a later point in time (Schütz et al., 2012). It is possible that this dynamic weighting of value and salience (Schütz et al., 2012) is only true for sudden stimulus onsets and that it might be different when visual information is continuously displayed – as it usually is in the real world. First, it might be that visual information and information about value still have to be combined and this combination process is only reflected in later saccade responses. A second possibility is that sudden onsets render stimuli highly salient (Gottlieb et al., 1998) and might increase the weight given to visual information for a certain period of time. If any of these two is true, then the relative contribution of value and relevance to oculomotor control can be increased by using continuously displayed stimuli at low contrast values. However, these scenarios, would need to be carefully evaluated and tested against each other, then they would provide instructive insights how valuation processes affect oculomotor control.

## 4.5 Conclusions

The present dissertation showed that the visual system integrates visual information acquired from pre-saccadic peripheral and post-saccadic foveal vision, weighs it according to its relative reliability and thereby maximizes all the information available. Thus, vision does not start anew with each fixation but can be described as a continuous integrated stream of information. In contrast to that, saccade latencies were not sensitive to the relative reliability of peripheral and foveal vision and thus did not to maximize the information available. Similarly, the third study of this dissertation showed that latencies of reactive saccades were not modulated by motivational value. The modulation of saccade latencies motivational value can only be found in contexts where the outcome depends on the participants' behavior.

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# Appendix

# Study I

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# Earlier saccades to task-relevant targets irrespective of relative gain between peripheral and foveal information

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**Saccades bring objects of interest onto the fovea for high-acuity processing. Saccades to rewarded targets show shorter latencies that correlate negatively with expected motivational value. Shorter latencies are also observed when the saccade target is relevant for a perceptual discrimination task. Here we tested whether saccade preparation is equally influenced by informational value as it is by motivational value. We defined informational value as the probability that information is task-relevant times the ratio between postsaccadic foveal and presaccadic peripheral discriminability. Using a gaze-contingent display, we independently manipulated peripheral and foveal discriminability of the saccade target. Latencies of saccades with perceptual task were reduced by 36 ms in general, but they were not modulated by the information saccades provide (Experiments 1 and 2). However, latencies showed a clear negative linear correlation with the probability that the target is task-relevant (Experiment 3). We replicated that the facilitation by a perceptual task is spatially specific and not due to generally heightened arousal (Experiment 4). Finally, the facilitation only emerged when the perceptual task is in the visual but not in the auditory modality (Experiment 5). Taken together, these results suggest that saccade latencies are not equally modulated by informational value as by motivational value. The facilitation by a perceptual task only arises when task-relevant visual information is foveated, irrespective of whether the foveation is useful or not.**

## Introduction

The human visual system comprises a large field of view with only a small and central region, the fovea, ensuring high visual acuity. In contrast to foveal vision, visual acuity in the periphery is comparatively poor. As a consequence, the fovea has to be oriented toward objects of interest to obtain detailed visual information. This is achieved by fast eye movements called saccades. The time it takes the eye to respond to an upcoming target (i.e., the latency), as well as other saccade dynamics (such as peak velocity) can be used to infer characteristics of visual processing and oculomotor control.

Eye movements are not only influenced by bottom-up factors like target contrast and color, but also by top-down factors like motivation (i.e., the desire to perform a particular action or achieve a certain outcome) and plans (e.g., Schütz, Lossin, & Gegenfurtner, 2015; Schütz, Trommershäuser, & Gegenfurtner, 2012; for reviews, see Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Schütz, Braun, & Gegenfurtner, 2011; Tatler, Hayhoe, Land, & Ballard, 2011). Saccades to rewarded targets show reduced latencies (Milstein & Dorris, 2007, 2011; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002) and increased peak velocities (Chen, Hung, Quinet, & Kosek, 2013; Takikawa et al., 2002). Milstein and Dorris (2007) found that saccade latencies to single targets are negatively correlated with the expected value (i.e., reward magnitude × reward probability) of a saccade target, and this correlation was stronger than a correlation with reward magnitude or reward probability only. In total, latencies to targets with high expected value were reduced by approxi-

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mately 40 ms compared to targets of low value. Milstein and Dorris (2007) concluded that expected motivational value is represented in oculomotor areas and influences the preparation of saccades. Motivation by reward can increase response speed without reducing accuracy, and thus can help to overcome the speed–accuracy trade-off (Manohar et al., 2015). A representation of expected value would thus be beneficial to speed up responses to rewarded targets and obtain rewards earlier without giving away accuracy. However, it can be argued that receiving a monetary reward for an eye movement is an artificial scenario, as eye movements naturally do not provide rewards but provide visual information about our environment.

The same benefit in eye movement latency of close to 40 ms and increased peak velocities can be observed when saccades are initiated in order to obtain information for a perceptual task (task-related saccade) compared to saccades that are merely elicited to fixate a target (target-elicited saccade) without the requirement for further information processing (Bieg, Bresciani, Bülthoff, & Chuang, 2012; Guyader, Malsert, & Marendaz, 2010; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). Montagnini and Chelazzi (2005) had their participants saccade to briefly presented targets and suggested that this benefit arose because the target was only presented briefly and perception would benefit from an early saccade. Bieg et al. (2012) showed that the effect persists if the target is displayed for longer durations, ruling out the urgency explanation. They suspected that the difference between task-related and target-elicited saccades might be related to motivational factors and that both saccade types are affected differently by repetitions. Another possibility that can explain the difference between task-related and mere target-elicited saccades is that the brain assigns a value to the information that can be obtained by executing the saccade, and that the preparation of saccades is modulated by this informational value in the same way as it is modulated by motivational value (Milstein & Dorris, 2007). This representation of informational value would help to obtain task-relevant information earlier and might affect the speed-accuracy trade-off in the same way as motivation by reward (Manohar et al., 2015).

To solve a perceptual task, we need to gather task-relevant information. The amount of information provided by a saccade depends on the target discriminability after the eye movement compared to target discriminability before the eye movement. For a saccade target, this corresponds to the relation between foveal and peripheral discriminability. Evidence that the oculomotor system utilizes information about the discriminability across the retina comes from optimal statistical models of eye movement planning (Najemnik & Geisler, 2005; Peterson & Eckstein, 2012; Renninger, Verghese, & Coughlan, 2007). These models assume that the visual system has information about its own sensitivity across the retina and optimizes information gain given its own constraints. However, these studies manipulated informational value indirectly and did not directly test whether the expected informational value is used in saccade preparation.

The aim of the current study was to investigate whether saccade latencies are modulated by the task-relevant information that can be obtained by saccade execution. If so, this would suggest that there is a representation of informational value, which can be used for the preparation of saccades. Moreover, it could explain the differences between mere target-elicited saccades and task-related saccades that are executed in order to sample task-relevant information. We define informational value, $value_{\text{inf}}$, as the product of information gain, $gain_{\text{inf}}$, and the probability that this information is task-relevant, $p_{\text{task}}$:

$$value_{\text{inf}} = gain_{\text{inf}} \times p_{\text{task}} \quad (1)$$

with the gain in information for a saccade being the ratio between postsaccadic foveal and presaccadic peripheral discriminability:

$$gain_{\text{inf}} = \frac{discriminability_{\text{fovea}}}{discriminability_{\text{periphery}}} \quad (2)$$

As a consequence of Equation 1, targets only carry informational value if they are task-relevant ($p_{\text{task}} > 0$). For any task-relevant target, the informational value increases with the gain in information, $gain_{\text{inf}}$. Whereas this information gain usually depends on the visual sensitivity across the retina, we here used a gaze-contingent display to independently manipulate foveal and peripheral discriminability and thus the gain in information a saccade provides (Experiments 1 and 2). In Experiment 3, we varied the task-relevance, $p_{\text{task}}$, while keeping the information gain, $gain_{\text{inf}}$, constant. In two further experiments, we confirmed that the difference between task-related and target-elicited saccades is spatially specific and not due to generally heightened arousal (Experiment 4) and we showed that the difference between the two saccade types does not emerge when the perceptual task is not in the visual but in the auditory modality (Experiment 5).

## Experiment 1: Manipulating information gain

If we saccade to any target that is relevant for a (perceptual) task, the execution of the saccade will lead to a gain in visual information, because spatial

resolution and sensitivity is usually superior in the fovea than in the periphery. In this experiment, participants had to saccade to a plaid stimulus and judge the orientation of its vertical component. We independently manipulated peripheral and foveal discriminability relative to previously determined individual thresholds. Both peripheral and foveal discriminability could be either above or below threshold, independently of each other. If saccades are influenced by the informational value for a perceptual task, then we would expect shorter saccade latencies when participants can gain information (periphery: below; fovea: above, B–A) compared to conditions where participants do not gain information, because peripheral and foveal discriminability are either both above or below threshold (A–A, B–B). Moreover, we would expect prolonged latencies (or even that participants do not execute saccades) when they lose information by making an eye movement; thus, when the foveal discriminability of the target is worse than the peripheral one (above to below, A–B). Individual discrimination thresholds in the fovea and the periphery were initially assessed during fixation (fixation task). Saccade latencies were then assessed without a perceptual task (saccade-only task) and with a perceptual task under different discriminability conditions (perceptual saccade task).

## Methods

### Participants

Observers were 19 undergraduate students from Giessen University. All observers were paid for participation (8 €/h) and had normal or corrected-to-normal vision. All experiments reported in this study were conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and were approved by the local ethics committee, LEK FB06, at Giessen University (proposal number 2013-0020). All observers gave informed consent prior to participation. Three participants were dismissed after completing the fixation task because their psychometric functions did not reach 90% performance. Thus, for the perceptual saccade task, we have a complete data set for 16 participants (mean age = 24.9 years; range: 19–31 years; 13 women, three men). Twelve of them (and one of the three discarded participants) had previously participated in the saccade-only task.

### Apparatus and stimuli

Stimuli were displayed using the Psychtoolbox (Brainard, 1997) in MATLAB (MathWorks, Inc., Natick, MA). For the first three participants, stimuli were displayed on a 21-in. SONY GDM-F520 CRT monitor with a refresh rate of 100 Hz. The monitor had a size of 37 × 29.6 cm, a spatial resolution of 1280 × 1024 pixel and was placed at 47 cm distance. For the remaining 13 participants, stimuli were displayed on a VIEWPixx monitor (VPixx Technologies, Saint-Bruno, QC, Canada) with a refresh rate of 120 Hz at a viewing distance of 48.5 cm. It had a spatial resolution of 1920 × 1080 pixel and a size of 51.5 × 29 cm. Eye movements of the right eye were recorded using the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002) and a tower-mounted EyeLink 1000 (SR Research Ltd., Ottawa, ON, Canada) with a sampling rate of 1000 Hz. Participant responses were recorded via a standard keyboard. As fixation cross, we used a combination of a bullseye and a crosshair with an outer diameter of 0.6° (Thaler, Schütz, Goodale, & Gegenfurtner, 2013).

Stimuli were plaids (i.e., sums of a vertical and horizontal grating), each with a spatial frequency of SF = 2 cycles per degree seen through a Gaussian window with a standard deviation of 0.4° of visual angle. Whereas the horizontal component was perfectly aligned to the cardinal axis, the vertical component was tilted clockwise (cw) or counterclockwise (ccw) by 10°. As changing the contrast of a Gabor patch influences its saliency and also its perceived size (Fredericksen, Bex, & Verstraten, 1997), we instead used a plaid and only varied the contrast ratio of both gratings while keeping the overall contrast constant. This allowed us to manipulate the discriminability of the task-relevant vertical component, without affecting saccade latencies via saliency. Contrasts of both patches added up to a fixed Michelson contrast of C = 0.4. For instance, a vertical contrast of 0.1 means that the horizontal contrast was 0.3. Hereafter, we report the contrast of the vertical component only. For the saccade-only task, vertical contrasts varied logarithmically in five discrete steps from 0.04 to 0.16. Contrast values in the perceptual saccade task were retrieved relative to individual psychophysical thresholds.

### Fixation task to determine individual thresholds

In the fixation task, plaid stimuli had a vertical contrast that varied in nine logarithmically spaced steps from 0.008 to 0.2 for the fovea, and from 0.028 to 0.25 for the periphery (method of constant stimuli). At the beginning of each trial, a centrally appearing fixation-cross signaled participants they could start a trial by pushing the space bar. After a random time of 750 to 1500 ms, the plaid appeared at the screen center replacing the fixation cross or at a horizontal eccentricity of 12.5° (left or right), in which case the fixation cross remained visible. Participants had to maintain fixation at the screen center. The plaid remained visible for 400 ms. A bar appeared that was randomly tilted

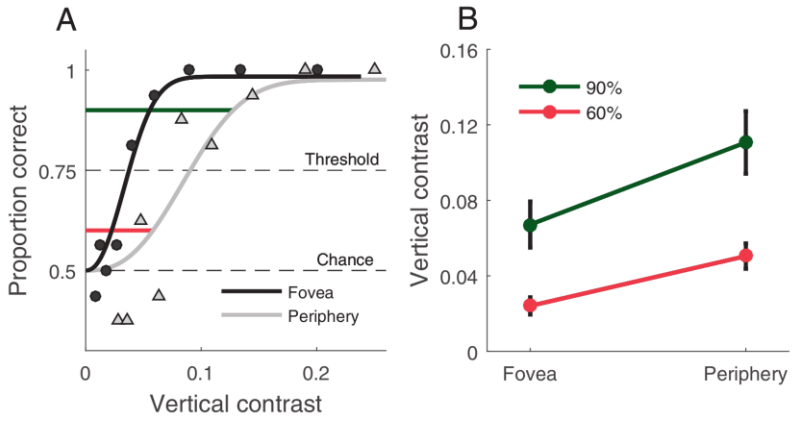


Figure 1. Experiment 1: Fixation task to determine peripheral and foveal contrast thresholds. (A) Psychometric functions for one exemplary observer. The red and the green line correspond to 60% and 90% correct, respectively. (B) Average vertical contrasts for the fovea and the periphery that correspond to 60% (red) and 90% (green) performance. Error bars are 95% confidence intervals.

either cw or ccw by 10° from the vertical axis indicating that participants now have to respond. By two additional buttons on the keyboard, participants could switch between the two possibilities and select the one that they thought matched the vertical plaid orientation (two-alternative forced choice; 2AFC). Participants received one point for a correct answer (+1), and minus one point (−1) for an incorrect answer. This score and their overall score was shown after each trial, separated by a vertical bar (e.g., +1 | 20). Additionally, a sound with a frequency of $f_{low} = 350$ Hz was played in case of a wrong answer. When participants did not maintain fixation, a sound with a higher frequency of $f_{high} = 500$ Hz was played. In total, the fixation task comprised 288 trials [9 (contrast values) × 2 (eccentricities) × 2 (orientations) × 8 (repetitions)], which were recorded in one session lasting about 40 min. This experiment was recorded in the same session directly after the saccade-only task.

Individual responses were transformed into proportion-correct choices for every stimulus value, separately for both viewing conditions (fovea, periphery). We then fitted Weibull functions to the data using Psignifit-4.0 software (Schütt, Harmeling, Macke, & Wichmann, 2016) and inverted them to retrieve contrast values, which correspond to 60% (below threshold) or 90% (above threshold) correct performance, respectively.

Figure 1A depicts psychometric functions for one observer; Figure 1B depicts average values for the above (A) and below (B) threshold values. On average, retrieved contrast values were higher in the periphery ($M = 0.081$, $SD = 0.02$) than in the fovea ($M = 0.046$, $SD = 0.015$), and higher for the above- ($M = 0.089$, $SD = 0.025$) than for below-threshold values ($M = 0.037$, $SD = 0.01$). To test that A and B values differ significantly, we entered the data in a 2 × 2 ANOVA with the factors eccentricity (fovea, periphery) and discriminability (above, below). Results reveal a main effect of discriminability, $F(1, 15) = 100.28$, $p < 0.001$, indicating that above values are higher than below values. Moreover, the main effect of eccentricity, $F(1, 15) = 72.74$, $p < 0.001$, shows that for identical performance less contrast is required for foveal than for peripheral vision. Due to a difference between the slopes of the foveal and peripheral psychometric functions, contrast differences between foveal and peripheral vision are larger for above- versus below-threshold values. This is reflected in the discriminability × eccentricity interaction, $F(1, 15) = 6.24$, $p = 0.025$.

### *Perceptual saccade task*

For the perceptual saccade task (Figure 2), participants were instructed to judge the vertical component of the plaid stimulus and that they may move their eyes. The trial initiation was identical to the fixation task. Plaid stimuli only appeared in the periphery and were displayed for 450 ms. The fixation cross remained visible for an additional 200 ms (overlap paradigm). The contrast of the plaid was derived from individual psychometric functions and could either be above (A) or below (B) peripheral threshold. As soon as the eye exceeded a distance of 2° from the fixation cross, the target was swapped to foveal contrast and could either be above (A) or below (B) foveal threshold for the remaining time. Afterward, participants had to respond via a keyboard press. As in the fixation task, participants received +1 point for a correct and −1

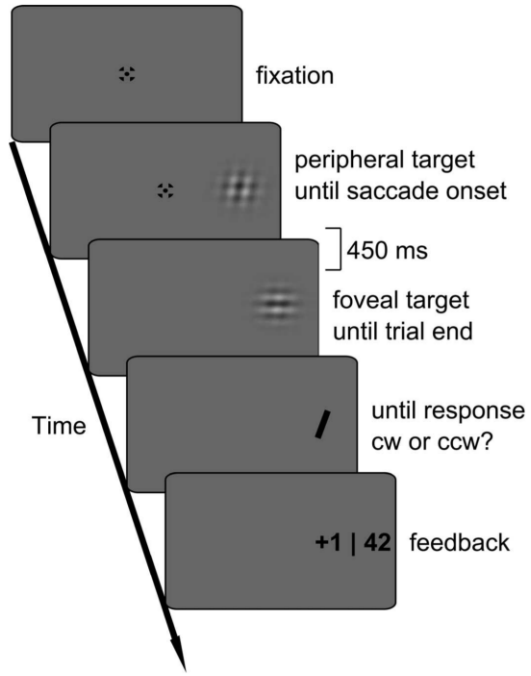


Figure 2. Experiment 1: Trial procedure for the perceptual saccade task. Participants fixated at the screen center and started each trial by pressing a button on a keyboard. After a random time between 750–1500 ms, a plaid appeared in the periphery. The plaid consisted of a horizontal sine wave aligned to the cardinal axis and a vertical sine wave that deviated by 10° either clockwise (cw) or counterclockwise (ccw). Participants were instructed to judge whether the orientation of its vertical component was cw or ccw and they were allowed to move their eyes. The contrast of the vertical relative to the horizontal component was either above or below the individual peripheral threshold. During the saccade, the relative contrast was adjusted to be either above or below the foveal threshold. The fixation cross was extinguished after 200 ms and the plaid was presented for 450 ms. Afterward, participants had to indicate the vertical orientation (cw or ccw) via a keyboard button press and received feedback. Stimuli are not drawn to scale.

point for an incorrect answer. This score and their overall score were shown after each trial, separated by a vertical bar (e.g., +1 | 20).

As peripheral and foveal discriminability could be above or below threshold, independent of each other, we had a $2 \times 2$ design with four possible conditions (A–A, A–B, B–A, B–B). The experiment consisted of four blocks with 200 trials each. In each block, we tested two of the conditions against each other. Conditions were arranged such that the target appeared to the left of fixation for the first condition and to the right of fixation for the second condition. This arrangement was counterbalanced across participants. Specifically, we tested A–A versus B–B, A–A versus B–A, B–A versus B–B, and A–B versus B–A. The whole experiment thus consisted of 800 trials and was recorded in one session, lasting between 1.5 and 2 h. Participants were told that blocks might differ with regard to difficulty, but they were neither informed about the gaze-contingent display nor about the specific conditions tested. After each block, participants often reported that the task at one of the two hemifields was particularly difficult, but they did not report the change of the target during the saccade.

### *Saccade-only task*

Thirteen of our 16 participants had previously participated in the saccade-only task. The trial procedure was identical to that of the perceptual saccade task, except that there was no perceptual task at the end of each trial. After the plaid had disappeared, the fixation cross immediately appeared at the screen center to indicate that participants could start the next trial. Participants were instructed to look as quickly as possible at the appearing plaid. Plaids could either appear in the left or right hemifield and the vertical component could either be tilted cw or ccw. Within a trial, the plaids' contrast did not change and belonged to one of five contrast values (vertical contrast: 0.04, 0.0566, 0.08, 0.1131, and 0.16). In total, participants completed two blocks of 160 trials each, which lasted between 20–30 min and were recorded in the same session as the fixation task.

### *Eye movement analysis*

Saccades were detected using the EyeLink 1000 (SR Research Ltd.) algorithm. Latencies were defined as the first saccadic sample with respect to target onset. To obtain peak velocities, we took the maximum of the differentiated eye position signals. In the perceptual saccade task, we removed trials with latencies below 100 ms and above 400 ms, which applied to 569 trials (4.5%). Latencies below 100 ms are likely to be caused by anticipation and not in response to the target, whereas with a latency above 400 ms, no foveal vision was provided as targets were presented for 450 ms. Removed trials were equally represented across conditions. We additionally discarded 211 further trials because the eye position was more than 2° away from the fixation cross while the target appeared (1.7%). Thus, our latency analysis is based on 12,020 of a total of 12,800 recorded trials (93.9%). For the analysis of peak velocities, we did not consider trials with missing samples during a saccade. This applied to a further 410

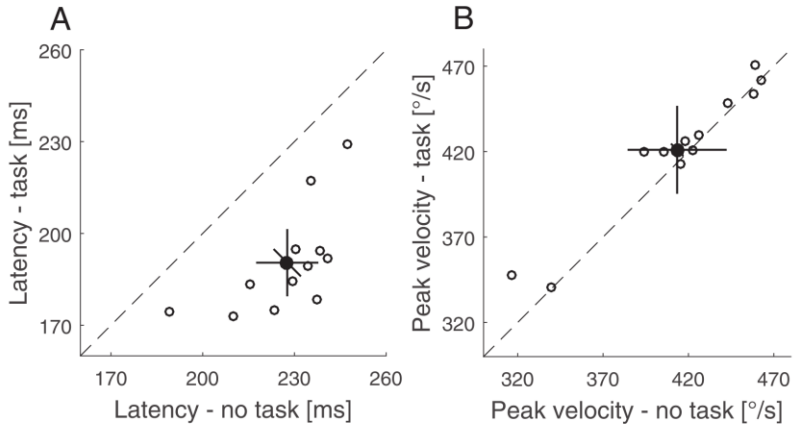


Figure 3. Experiment 1: Effect of a perceptual task. Saccade latency (A) and peak velocity (B) averaged across all four perceptual saccade task conditions (task) against values from the saccade-only task (no task). Black circles are averaged data with 95% confidence intervals. Diagonal error bars mark the error of the differences between the two conditions and have to be compared to the identity line. Open circles denote data from individual observers.

trials. The same criteria applied to the saccade-only task. Here, 336 of 4,160 trials (8.1%) were discarded as their latencies were not in the given time window, and additional 118 trials were not considered for the analysis of peak velocities.

## Results

### *The effect of a perceptual task*

In the saccade-only task, the average saccade latency was 226 ms ($SD = 16$ ms) and latencies did not vary as a function of the plaids' contrast ratio. Average latencies for the five different contrast values were 226, 223, 228, 226, and 226 ms when the contrast of the vertical grating was 0.04, 0.057, 0.08, 0.113, and 0.16. A linear regression of the saccade latencies on these contrast values revealed a slope of $b = 4.4$ ms. Thus, according to the regression, changing the contrast from 0.04 to 0.16 would increase the latency by about 0.5 ms. A one-way repeated measures ANOVA also revealed that the contrast ratio of the plaids did not influence saccade latencies ($F < 1$). Average and individual latencies from the perceptual saccade task and the saccade-only task can be found in Figure 3A. With a perceptual task, the average saccade latency decreased by 36 ms to 190 ms, $t(11) = 9.17$, $p < 0.001$ (range: 15–60 ms).

We also found higher peak velocities with ($M = 421$ °/s, $SD = 41$ °/s) compared to without-perceptual task ($M = 413$ °/s, $SD = 45$ °/s), $t(11) = 2.33$, $p = 0.04$ (Figure 3B). According to the saccadic main sequence, peak velocities are known to increase with saccade amplitudes (Bahill, Clark, & Stark, 1975), so we assessed whether this difference in velocities was caused by a difference in amplitudes. Therefore, we first compared saccade amplitudes in the perceptual saccade ($M = 12.16°$, $SD = 0.15°$) and the saccade-only task ($M = 12.05°$, $SD = 0.23°$). We did not find any statistical evidence for larger amplitudes with a perceptual task at hand, $t(11) = 2.03$, $p = 0.067$. However, an absence of statistical significance is not evidence that amplitudes are actually identical. Furthermore, the amplitude difference was in the same direction as the difference in peak velocity, as expected by the main sequence. Therefore, we also computed a velocity index that was corrected for amplitude. The velocity index, $V_I$, was defined as the saccade's peak velocity divided by the square root of its amplitude (Lebedev, Van Gelder, & Tsui, 1996). Mean velocity indices, $V_I$, were 121 ($SD = 11$) with and 119 ($SD = 13$) without perceptual task and did not differ significantly, $t(11) = 1.56$, $p = 0.147$. Moreover, and unlike the study by Bieg et al. (2012), we did not find any evidence for decreasing latency differences and increasing peak velocity differences over the duration of the experiment (Supplementary Figure S1).

### *The effect of peripheral and foveal discriminability*

We entered saccade latencies from the perceptual saccade task (Figure 4A) in a $2 \times 2$ ANOVA with the factors foveal and peripheral discriminability, both with the levels above and below. If saccade latencies were modulated by information gain, this would have resulted in a significant interaction. The ANOVA

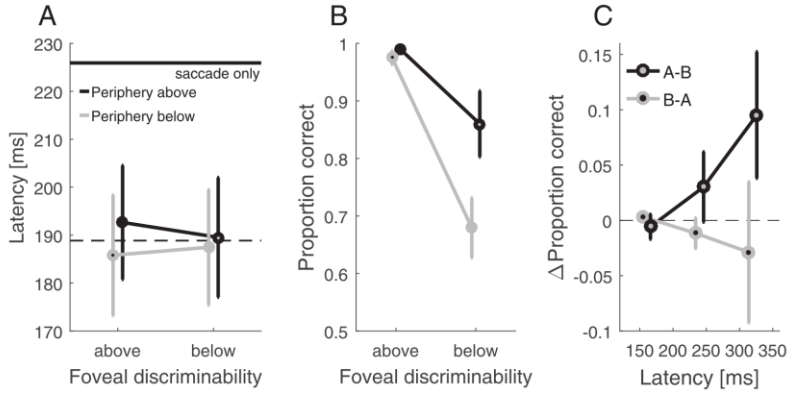


Figure 4. Experiment 1: Effect of peripheral and foveal discriminability. (A) Average saccade latencies in the four different conditions. Error bars are 95% confidence intervals of between-participant variability. The dashed horizontal line represents the average latency in all conditions with a perceptual task, and the solid black line represents the average latency without a perceptual task. (B) Average perceptual performance for the four different conditions, with error bars denoting 95% confidence intervals. (C) Relative performance as a function of latency in the perceptual saccade task for the A–B and B–A condition. Proportion of correct responses subtracted by the individual mean in each condition for three 80 ms bins centered on 160, 240, and 320 ms. Error bars denote 95% confidence intervals of between-participant variability. Values are slightly offset for better visibility.

revealed a main effect of peripheral discriminability, $F(1, 15) = 8.54$, $p = 0.011$. Saccade latencies were lower by about 4 ms when the peripheral discriminability was below ($M = 187$ ms, $SD = 25$ ms) compared to above threshold ($M = 191$ ms, $SD = 24$ ms). We neither observed a main effect of foveal discriminability, $F(1, 15) = 0.16$, $p = 0.698$, nor an interaction, $F(1, 15) = 2.25$, $p = 0.154$. For peak velocities, no differences were observed (all $F < 1$).

One possible explanation for the absence of a noteworthy latency modulation would be that our manipulation of target discriminability did not affect perception in the first place. If our manipulation was successful, then (a) performance should differ across the different conditions, and (b) performance in the B–A and the A–B conditions should depend on the saccade latency. To confirm that our manipulation of target discriminability was indeed successful, we first compared performance across the different contrast conditions (Figure 4B). Performance was best in the A–A condition ($M = 0.99$, $SD = 0.01$), worst in the B–B condition ($M = 0.68$, $SD = 0.10$), and intermediate for the A–B ($M = 0.86$, $SD = 0.11$) and the B–A ($M = 0.98$, $SD = 0.02$) conditions. A nonparametric Friedman test of repeated measures revealed that performance in the conditions differed significantly, $X^2 = 36.84$, $p < 0.001$. In order to test whether performance was better with above-threshold foveal information, we compared performance in the A–A condition with the A–B condition and the B–A condition with the B–B condition using Wilcoxon signed rank tests. Performance in the A–A condition was significantly better than in the A–B condition, $Z = -3.35$, $p < 0.001$, and performance in the B–A condition was significantly better than in the B–B condition, $Z = -3.41$, $p < 0.001$. To test effects of peripheral discriminability, we compared performance in the B–A with A–A conditions as well performance in the B–B with the A–B conditions. With below-threshold foveal information, above-threshold peripheral information improved performance, B–B versus A–B: $Z = -3.29$, $p < 0.001$. When foveal information was above threshold, the performance benefit due to peripheral discriminability failed to reach significance, A–A versus B–A, $Z = -2.45$, $p = 0.014$ (Bonferroni-corrected alpha level: $\alpha' = 0.0125$).

The second important prediction from our manipulation was that performance in the A–B condition as well as the B–A condition should depend on the saccade latency: When peripheral information is above threshold and foveal information is below threshold (A–B), performance should increase with higher latencies, because above-threshold peripheral information would be available for a longer duration. It should be the other way round for the B–A condition. To test this prediction, we split the data into three 80 ms bins centered on 160, 240, and 320 ms. For each participant in every bin, we computed the proportion correct relative to the individual mean in the respective condition (Figure 4C). We compared the data using a 3 (latency bins) × 2 (conditions) repeated-measures ANOVA. The ANOVA revealed a significant latency

bin × condition interaction, $F(2, 18) = 6.73$, $p = 0.007$, suggesting that performance depended on the saccade latency. To quantify how much participants would have benefitted by adjusting their reaction time, we computed linear regressions on the relative performance values over the three latency bins. Relative performance values were averaged across participants. The regressions revealed a slope of $b_{A-B} = 0.63\ s^{-1}$ for the A–B and a slope of $b_{B-A} = -0.20\ s^{-1}$ for the B–A condition. This suggests that by delaying a saccade from the fastest percentile (113 ms) to the slowest percentile (332 ms), participants' performance would have increased by 13.8% in the A–B condition and it would have decreased by 4.4% in the B–A condition.

## Discussion

We measured saccade latencies to plaid stimuli, which also served as target for a perceptual task. With a perceptual task, latencies were reduced by 36 ms compared to a saccade task without perceptual judgment. The magnitude of the latency difference between task-related and target-elicited saccades reported here is in line with previous findings (Bieg et al., 2012; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). Additionally, we independently manipulated peripheral and foveal discriminability of the plaids task-relevant vertical component by changing its contrast during the saccade. Saccade latencies were not modulated by information gain, but they were lower by about 4 ms when peripheral contrast was below threshold. Compared to the 36-ms facilitation by a perceptual task, this effect is negligibly small and we conclude that the differences in information gain do not modulate the facilitating effect of a perceptual task.

We also found higher peak velocities when the saccade was accompanied by a perceptual task. Although there was no statistical difference in amplitudes, this peak velocity effect vanished when corrected for saccade amplitude (Lebedev et al., 1996). Therefore, we cannot dismiss the possibility that the difference in peak velocity is confounded with tiny yet systematic differences in amplitude. One possible analysis to avoid this confound would have been to look at the whole main sequence relationship between amplitude and peak velocity (Bahill et al., 1975). As we were primarily interested in latency effects, we did not vary saccade amplitude and are therefore not able to explore the main sequence relationship.

Bray and Carpenter (2015) recently reported reduced latencies to informative targets. They varied whether a first saccade target (colored dot) reliably indicated the position of the second saccade target or not. They labeled the reliable first target as being an informative target and the unreliable one as being an uninformative target. In their experiment, latencies are reduced when the target reliably indicates the destination of the forthcoming saccade (Bray & Carpenter, 2015). However, their definition of informativeness differs drastically from ours. Whereas their definition concerns the external reliability of a saccade target, our definition of information gain involves the internal comparison of foveal and peripheral vision and thus, the informativeness of the saccade itself given the constraints of the visual system. In contrast to that, their task (Bray & Carpenter, 2015) does not necessarily involve the comparison of peripheral and foveal vision, but could be solved with peripheral vision alone.

The independent manipulation of peripheral and foveal discriminability in our experiment also changed how much information observers gathered by executing a saccade. The condition in which the plaid was presented below threshold in the periphery but changed to above threshold once foveated (B–A) mimicked normal saccades, in which people gained information by making saccade eye movements. The opposite is true for the A–B condition, in which people actually lost information by executing the saccade. Performance in the B–A condition indeed decreased with increasing latency and it increased with increasing latency in the A–B condition. Because participants were only instructed to solve the task and had 450 ms to discriminate the target, the optimal response in the A–B condition would have been to delay the saccade as much as possible or to not saccade to the target at all. Nevertheless, observers neither omitted the saccade, nor did they delay their eye movement in order to benefit longer from peripheral vision.

In order to compute a saccade's gain in information, the visual system would have to compare the presaccadic peripheral and postsaccadic foveal discriminability. Since foveal information is only available after executing the saccade, the information gain has to be estimated before saccade preparation based on the predicted foveal information. This prediction would then have to be updated over the time course of the experiment. It might be that this learning did not take place, although prior research showed that the oculomotor system is generally able to adjust the distribution of reaction times given the constraints of a task (Jarvstad, Rushton, Warren, & Hahn, 2012; Madelain, Champrenaut, & Chauvin, 2007; Schütz et al., 2012). Moreover, computing the information gain would require a separate representation of information obtained from peripheral and foveal samples of the stimulus. Such a separate representation would not be given when the information from both samples is combined into a single representation of the object and its features. Thus, one possible explanation why latencies did not differ across conditions might be that the oculomotor system does not have separate access to

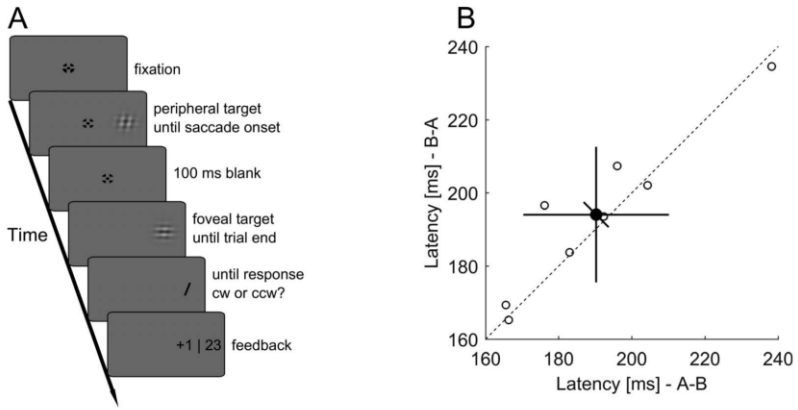


Figure 5. Experiment 2: Effect of peripheral and foveal discriminability with target blanking. (A) The trial procedure for Experiment 2 was identical to the perceptual saccade task in Experiment 1 (Figure 2), with the only exception being the introduction of a 100-ms blank during the saccade. The target (including blank) was presented for 550 ms. (B) Average latency in the B–A versus latency in the A–B condition. Diagonal error bars mark the error of the difference between the two conditions, and have to be compared against the diagonal. Open circles denote individual data.

peripheral and foveal discriminability because both the peripheral and foveal information are integrated into a common trans-saccadic percept (Ganmor, Landy, & Simoncelli, 2015; Wolf & Schütz, 2015).

## Experiment 2: Target blanking

In Experiment 1, we replicated the finding that saccade latencies are reduced whenever people engage in a perceptual discrimination task at the saccade target. Furthermore, the present results show that this facilitation was not modulated by peripheral and foveal discriminability. As mentioned above, one possible explanation might be that participants integrated peripheral and foveal information (Ganmor et al., 2015; Wolf & Schütz, 2015) and therefore lost separate access to peripheral and foveal information. If peripheral and foveal information is not accessible separately, the gain or loss of information by a saccade cannot be computed and as a consequence cannot modulate saccade latencies. Thus, we wanted to guarantee in Experiment 2 that participants do not integrate peripheral and foveal information, but have separate access to peripheral and foveal discriminability. Therefore, we introduced a target blank shortly after the eye landed. Blanking the target is known to make information from pre- and postsaccadic samples separately accessible (Deubel, Schneider, & Bridgeman, 1996; Weiß, Schneider, & Herwig, 2015).

### Methods

We recorded data from nine participants who were all undergraduate students from Giessen University. Data from one participant were excluded from the analysis because more than 80% of trials were corrupted with blinks. The remaining eight participants whose data were considered for the analysis had a mean age of 21 years (range: 18–24 years; seven women, one man). The setup was identical to the previous experiment. We measured saccade latencies to peripherally appearing plaids in an above to below (A–B) and a below to above (B–A) threshold condition (Figure 5A). Again, the contrast of both gratings added up to 0.4 and the vertical contrast was set to the average values derived from Experiment 1 (Figure 1B). Specifically, in the A–B condition, the vertical contrast was set to 0.111 for peripheral and 0.024 for foveal vision. In the B–A condition, it was set to 0.05 (periphery) and 0.067 (fovea). The trial procedure was identical to Experiment 1 with the only exception being that the target disappeared for 100 ms (blank) as soon as the eyes exceeded the critical distance of 1.5° from the fixation cross. Afterward, the target was displayed at foveal contrast until the end of the trial (450 ms after target onset). Identical to Experiment 1, participants had to indicate the orientation of the vertical component which was tilted cw or ccw. Data from the A–B and the B–A conditions were obtained in the same session, and for every observer, one condition was assigned to each hemifield. This assignment was balanced across participants. The experiment com-

prised 400 trials and lasted approximately one hour. We discarded trials with an eye movement latency below 100 ms and above 400 ms. In total, 95.4 % of trials were considered for the final analysis.

### Results

Figure 5B depicts average saccade latencies in both conditions for every observer. In the A–B condition, the average saccade latency was 190 ms ($SD = 23$ ms), in the B–A condition, it was 194 ms ($SD = 22$ ms). We found no significant difference between latencies in the A–B and the B–A condition, $t(7) = 1.33$, $p = 0.23$. In the A–B condition, performance was 80% correct ($SD =$ 18%), whereas in the B–A condition, participants achieved 97% correct responses ($SD = 2\%$). A Wilcoxon signed rank test revealed that performance differed significantly between the two conditions, $Z = -2.24$, $p =$ 0.025.

### Discussion

Here we tested whether the manipulation of information gain affects saccade latencies when a blank is included between the peripheral and foveal target. Target blanking is known to make information from peripheral and foveal samples separately accessible (Deubel et al., 1996; Weiß et al., 2015). We tested one condition wherein observers gained information (B–A) against another condition in which they lost information by making a saccade (A–B). As in Experiment 1, we did not find any evidence for information gain influencing saccade preparation. This means that the lack of an effect could not be explained by potentially mandatory integration of peripheral and foveal information (Ganmor et al., 2015; Oostwoud Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015).

## Experiment 3: The probability of a perceptual task

Milstein and Dorris (2007) found a linear relationship between saccade latencies to single targets and the expected value associated with those targets. Expected value can be computed as the product of reward magnitude and reward probability. Milstein and Dorris (2007) independently manipulated these two factors to obtain targets with different expected values. Saccade latencies correlated with both reward magnitude and probability, but best with expected value—the combination of the two. In Experiments 1 and 2 we have shown that saccade latencies did not depend on the gain in information (in contrast to reward magnitude). In all our perceptual task conditions, the probability of a perceptual task was always unity. Thus, the informational value was identical to the gain in information. In this experiment, we want to test whether the second factor in Equation 1, task probability, affects saccade preparation and yields a linear relationship with saccade latencies.

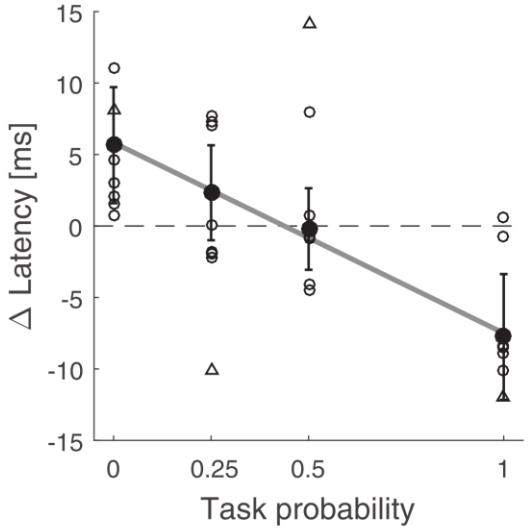


Figure 6. Experiment 3: Effect of task probability. Latency relative to individual mean as a function of task probability with 95% between-participant variability. Open circles denote individual data. Open triangles are data from the participant who was labeled an outlier. The solid gray line is a linear regression through the aggregated data (slope: −13.3 ms).

### Methods

We recorded data from eight observers, the same observers who also completed Experiment 2. Data from one participant was not included in the final analysis because the average latency in two conditions deviated by more than 2 standard deviations (Figure 6, open triangles). Stimuli were again plaid stimuli with a vertical contrast of 0.05. The experiment consisted of four blocks of 200 trials each. Within each block, targets could appear either on the right or on the left side of the screen. Participants were instructed to saccade to the target and, if applicable, report its orientation. They were told that the blocks differ with regard to the probability that they will have to respond. At the end of the trial, either the fixation cross appeared at the screen center to show that they may

continue with the next trial or a bar appeared at the target position to show that they have to report the orientation of the vertical component. Within one block, there was one fixed probability that observers had to respond. Task probabilities were 0, 0.25, 0.5, and 1. Again, we discarded trials with too early (<100 ms) or too late (>400 ms) saccades. This applied to 255 trials (9.1%).

### Results

For every observer in every probability condition, we computed the average latency relative to the individual mean across conditions. The average latency differences decreased with increasing task probability from 5.7 ms ($p_{task} = 0$, $SD = 6$) over 2.3 ms ($p_{task} = 0.25$, $SD = 5$) and −0.2 ms ($p_{task} = 0.5$, $SD = 4$) to −7.7 ms ($p_{task} = 1$, $SD = 6$). Average and individual values are depicted in Figure 6. We compared saccade latencies using a repeated-measures ANOVA with the factor task probability. The ANOVA revealed a significant main effect of task probability, $F(3, 18) = 5.96$, $p = 0.005$. We determined the mean latency for each task-probability condition by averaging across all observers and computed a regression of these mean latencies on task probability. The regression revealed a slope of −13.3 ms and explained 99% of variance.

### Discussion

The present experiment tested whether saccade latencies decrease linearly with the probability that information obtained at the saccade target is task-relevant. Participants saccaded to plaid stimuli in the periphery. Across blocks, we varied the probability that observer had to report the orientation of the plaids' vertical component. We found that the probability of a perceptual task affected saccade latencies. Latencies decreased linearly with increasing task probability.

The average latency difference when observer had to respond throughout ($p_{task} = 1$) and the condition without perceptual task ($p_{task} = 0$), yielded a value of 13.3 ms. This difference is smaller than in the results of Experiment 1 and the values reported in the literature (Bieg et al., 2012; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). One possible explanation might be that observers did not represent the task probabilities veridically, but instead biased them towards the mean task probability. This would agree with classic findings on the misrepresentation of extreme probabilities outlined in prospect theory (Kahneman & Tversky, 1979). Thus, observers might have expected a perceptual task even in the zero probability condition and they might have expected the absence of a perceptual task even in the 100% condition.

## Experiment 4: The perceptual task effect is spatially specific

In Experiment 3, we found that the facilitation due to a perceptual task is modulated by task probability. Because task probability within one block was the same for both hemifields, we do not yet know whether this facilitation is spatially selective or caused by global arousal. If the facilitation was not spatially selective, it could explain the absence of a noteworthy latency modulation in Experiment 1. In Experiment 1, we always tested two conditions of different information gains against each other, one assigned to each hemifield. As a consequence, differences might have averaged out. In this experiment, we aim to show that our results are not affected by global arousal but that the perceptual task effect is spatially specific.

### Methods

Participants were five undergraduate students from Giessen University (mean age: 26 years; age range: 20–30 years; four women, one man). All of them had previously participated in Experiment 1. The setup was identical to the previous experiments. The plaids contrast was set to the individual peripheral below threshold value from Experiment 1 and not modified during a trial or the experiment. Two observers had to perceptually respond whenever the plaid appeared on the left, and the remaining three observers had to perceptually respond to targets in the right hemifield. The experiment consisted of 200 trials and lasted approximately 30 min. We removed 89 out of 1,000 trials for the final analysis due to too early or too late saccade onsets.

### Results

Figure 7 depicts individual latencies in the saccade-only and the perceptual saccade task, both from the present experiment, in which both tasks have been interleaved, as well as from Experiment 1, in which they had been recorded in separate blocks. In the present experiment, the average latency is 183.8 ms ($SD = 10.7$ ms) in the perceptual saccade task and 220.3 ms ($SD = 19.7$ ms) in the saccade-only task. Latencies were thus reduced by 36.5 ms due to the presence of a perceptual task. Latencies for the same individuals from Experi-

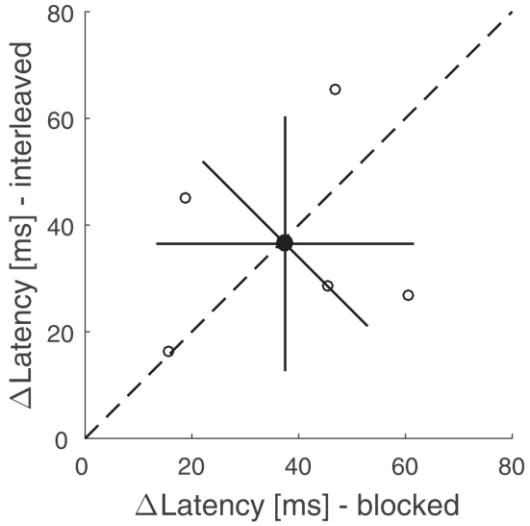


Figure 7. Experiment 4: Spatial specificity of perceptual task. Latency difference between the saccade-only task and perceptual saccade task when both have been recorded in separate blocks against when both have been recorded in the same block. Diagonal error bars mark the error of the difference between the two conditions and have to be compared against the diagonal. Open circles denote individual data.

ment 1 are 199.1 ms ($SD = 23.5$ ms) in the perceptual saccade task and 236.6 ms ($SD = 6.6$ ms) in the saccade-only task. This corresponds to a difference of 37.5 ms. We entered the data into an ANOVA with the two-factors task versus no task and blocked versus interleaved. We obtained a significant main effect of task versus no task, $F(1, 4) = 31.18$, $p = 0.005$. There was neither a significant main effect of blocked versus interleaved, $F(1, 4) = 5.64$, $p = 0.076$, nor a significant interaction, $F < 1$. A Wilcoxon signed rank test revealed that latencies were significantly shorter in the perceptual saccade task, $Z = -2.02$, $p = 0.043$.

### Discussion

In this experiment, we have tested whether the effects of a perceptual task are spatially specific. We have compared saccade latencies to one hemifield where participants had to do a perceptual task against latencies to the other hemifield without perceptual task. If the perceptual task effect was caused by arousal, then the latencies to both sides should be similar. We again found shorter saccade latencies to targets that also served as targets for a perceptual task. The latency difference was 36.5 ms and thus in the same magnitude as in Experiment 1 and previous studies (Bieg et al., 2012; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). We hereby have replicated the finding that the perceptual task effect is spatially selective and not caused by arousal (Montagnini & Chelazzi, 2005).

## Experiment 5: Auditory perceptual task

So far, we have shown that the perceptual task effect is modulated by the probability of a perceptual task and that the facilitation is spatially specific. Thus, it might be caused either by the requirement to foveate task-relevant information and process it with high acuity, or by a general motivation to solve perceptual tasks. In the latter case, shorter latencies should also be observed when the perceptual task is in any modality other than the visual one.

In this experiment, we tested whether saccade latencies are also affected by the presence of an auditory task. Participants saccaded to plaid stimuli and either had to discriminate tones (saccade and auditory task) or ignore them (saccade-only task). Half of the participants had to discriminate a tone that was played as long as the saccade target (continuous tone), the other half had to discriminate a tone that was played as soon as they foveated the saccade target (foveated tone). Continuous tones are equivalent to visual stimuli with regard to their presentation time, whereas foveated tones mimic the foveation behavior of saccades.

### Methods

Participants were eight undergraduate students from Marburg University aged between 20 and 26 years (mean age = 23 years; $SD = 2$; six women, two men). None of them had taken part in any of the previous experiments. We recorded eye movements of the right eye using a desktop mounted EyeLink 1000 (SR Research Ltd.) with a sampling rate of 1000 Hz, and the Eyelink Toolbox (Cornelissen et al., 2002). Participant responses were recorded via a standard keyboard. Tones were played via Sennheiser HD 280 Pro headphones (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany).

Participants had to saccade to plaid stimuli either left or right from fixation (Figure 8A). The contrast of the vertical and horizontal components again summed up to 0.4, with the contrast of the vertical component set to 0.2. The horizontal component was aligned to the cardinal axis whereas the vertical component was tilted cw or ccw by 10°. The plaid was continuously displayed

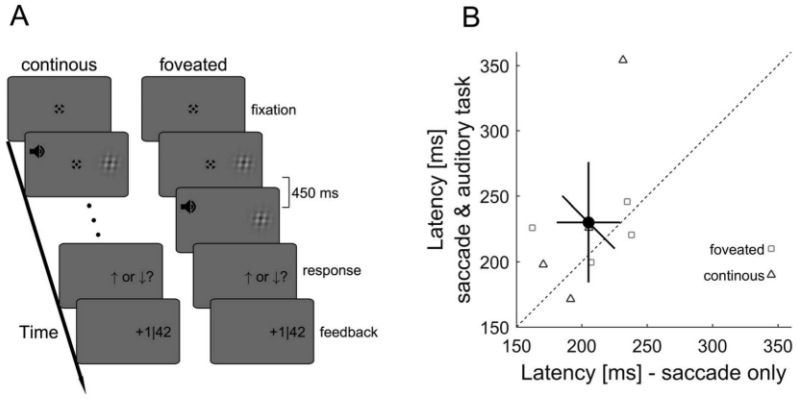


Figure 8. Experiment 5: Effect of auditory perceptual task. (A) Trial procedure for the two auditory perceptual tasks. In the continous condition, tones were displayed for 450 ms along with the plaid, whereas in the foveated condition, tones were displayed for 100 ms upon foveation of the saccade target. (B) Average and individual latencies in the saccade and auditory task compared to the saccade-only task.

for 450 ms. For half of the participants, a tone was played for 100 ms when they had foveated the plaid (foveated tone; approx. 60 ms after saccade onset) and for the remaining half, it was played as long as the plaid was presented on the screen (continuous tone). Tones were pure tones varying in 8 steps around 440 Hz (396, 418, 429, 434.5, 451, 462, 484, 528) for foveated tones and around 220 Hz (198, 214, 214.5, 217.25, 225.5, 231, 242, 264) for continuous tones. The experiment consisted of two blocks of 200 trials each: One block in which participants were instructed to saccade to the plaid and ignore the tone (saccade-only task) and another block in which participants had to discriminate whether the tone belonged to the higher or to the lower frequencies (saccade and auditory task). For foveated tones, participants were instructed to discriminate the target and were told that the tone was played as soon as the plaid was foveated. For continuous tones, observers were instructed to foveate the plaid and discriminate the tone. The order of conditions was balanced across participants. Every observer completed a practice session of eight trials, which were not included in the analyses. Eye movement analyses were identical to Experiment 1. We discarded 349 out of 3,200 trials due to too short (<100 ms) or too long (>400 ms) latencies. This corresponds to 10.9 % of trials.

On average, observers correctly identified the tones in 86.9 % of trials ($SD = 4.6\%$, range: 80.7%–93.4%). Performance for foveated tones ($M = 86\%$, $SD = 4.7\%$) and continuous tones were in a similar range ($M = 87.8\%$, $SD = 5.1\%$). We converted individual responses into "proportion higher" for each frequency and fitted a cumulative Gaussian to the data using Psignifit-4 (Schütt et al., 2016). Weber fractions (i.e., standard deviation of the Gaussian divided by the central frequency) were $M = 6.3\%$ ($SD = 1.9\%$). This value is in the range of Weber fractions for pitch discrimination among young healthy individuals (Moore & Peters, 1992).

## Results

Saccade latencies for the saccade-only and the saccade and auditory task are depicted in Figure 8B. They were $M = 205$ ms ($SD = 29$ ms; range: 162–238 ms) in the saccade-only task and $M = 230$ ms ($SD = 55$; range: 171–354 ms) in the saccade and auditory task, $t(7) = 1.47$, $p = 0.185$. To test the hypothesis that saccadic reaction time benefits are only present for visual but not for auditory perceptual tasks, we analyzed the present results together with the perceptual (i.e., visual) saccade task and the saccade-only task from Experiment 1. We entered individual mean latencies for the visual and auditory task and the saccade-only tasks in a $2 \times 2$ ANOVA. The ANOVA comprised the between-participants factor modality (visual vs. auditory) and the within-participant factor perceptual task (absent vs. present). If there is no benefit for auditory tasks, then we should observe a modality $\times$ perceptual task interaction. The ANOVA revealed a significant interaction, $F(1, 18) = 18.25$, $p < 0.001$. No other effects were observed in the ANOVA (all $F < 1$). The interaction remained significant ($p < 0.001$), even when one participant with extremely high latencies in the auditory task condition was excluded from the analysis (top data point in Figure 8).

### Discussion

Here we asked whether the perceptual task effect is restricted to the foveation of visual information or whether it is caused by the motivation to solve a task and therefore also appears with a task in any other than the visual modality. Contrary to the visual modality (Experiment 1), we found no evidence for shorter latencies when participants had to discriminate tones that were either played simultaneously with the saccade target or upon foveation of the saccade target. We conclude that the perceptual task effect is a pure visual phenomenon and thus that shorter saccade latencies are only observed when task-relevant information has to be processed with the fovea.

## General discussion

The present study was designed to investigate whether informational value modulates the preparation of saccades similarly as expected motivational value does and whether this can explain the shorter saccade latencies that go along with a perceptual task. We found shorter saccade latencies with than without perceptual task, but this perceptual task effect was not modulated by the information saccades provide in terms of discriminability (Experiments 1 and 2). Saccade latencies decreased with increasing probability of a perceptual task at the saccade target (Experiment 3), and the perceptual task effect vanished when the perceptual task was not in the visual modality but in the auditory modality (Experiment 5). Taken together, our findings suggest that informational value is not used for the preparation of saccade eye movements in an extent comparable to motivational value (Milstein & Dorris, 2007).

### The influence of perceptual value on eye movements

A currently discussed question in eye movement research is whether eye movements support perception optimally; that is, whether they maximize the gain in information and thus minimize perceptual uncertainty. One crucial requirement for optimal eye movement control would be a representation of visual uncertainty across the visual field. The fact that people are able to choose the less uncertain stimulus for perceptual judgments (Barthelmé & Mamassian, 2009, 2010) and that peripheral and foveal target information contribute to transsaccadic perception in inverse proportion to their uncertainty (Ganmor et al., 2015; Wolf & Schütz, 2015) suggests that humans do represent perceptual uncertainty and that this information can be used for perception. Although information about uncertainty seems to be available in the perceptual system, it does not seem to be used consistently to optimize eye movement control. Some studies found that eye movements maximize information gain (Hoppe & Rothkopf, 2016; Najemnik & Geisler, 2005; Peterson & Eckstein, 2012, 2013), while other studies found clearly suboptimal eye movement behavior (Morvan & Maloney, 2012; Verghese, 2012) or mixed results (Eckstein, Schoonveld, Zhang, Mack, & Akbas, 2015; Renninger et al., 2007; Schütz et al., 2012). Another study (Ackermann & Landy, 2013) showed that the endpoints of initial saccades are clearly biased by the expected value to correctly locate a target in a rewarded target region, but endpoints are not optimal with regard to the gain in information. These widely different results suggest that the optimality of eye movements might depend very much on the task and the stimuli.

In the current study, we did not find any evidence that this information is used to modulate and optimize the preparation of saccades. If eye movements supported perception optimally, we should have observed shorter latencies when people can gain information by making an eye movement and longer latencies when people cannot gain or actually can lose information. Instead, latencies tended to be similar across all conditions of information gain. Theoretically, all relevant information was available in our paradigm and could have been used for eye movement control. In fact, we showed previously in a very similar paradigm, that the visual system has access to peripheral and foveal uncertainty (Wolf & Schütz, 2015). However, this information did not modulate saccade latencies, not even with a target blank that makes peripheral and foveal information even more accessible. Moreover, the fact that participants continued to execute saccades in the A–B condition when doing so deteriorated their perceptual performance suggests that foveation of task-relevant information is an overlearned and rigid behavior. This behavior might be reinforced by the regular experience of gaining information with foveal vision (Paeye, Schütz, & Gegenfurtner, 2016). Although previous studies showed that learning can shape reaction time distributions (Madelain et al., 2007); that participants are sensitive to the difficulty of a task and can adjust their reaction times accordingly (Jarvstad et al., 2012); or that they can adjust their latencies to increase reward (Schütz et al., 2012), there seems to be a strong urge to directly foveate a target even if this is clearly suboptimal for completing the task at hand (Morvan & Maloney, 2012).

Overlearned and rigid foveation behavior is also reflected in findings with simulated visual field loss. When a central scotoma is simulated, objects can no further be identified with foveal vision. Consequently,

visual search performance is deteriorated drastically (Cornelissen, Bruin, & Kooijman, 2005; Nuthmann, 2014), and compensating for the scotoma requires long-lasting training (Sommerhalder et al., 2004). An exception from this rigid foveation seems to be visual search under scotopic conditions, as eye movement behavior is partially adjusted to the functional scotoma in the fovea during scotopic vision (Paulun, Schütz, Michel, Geisler, & Gegenfurtner, 2015).

The fact that we tested reactive saccades in response to unpredictable, sudden onsets in the periphery might have contributed to the rigid and suboptimal behavior. Typically, saccades with short latencies are less efficient than saccades with longer latencies (Ghahghaei & Verghese, 2015; Markowitz, Wong, Gray, & Pesaran, 2011; Schütz et al., 2012). In that sense, the general facilitation by the perceptual task might be even counterproductive in our paradigm and prevent an appropriate control of saccades by informational value.

### The facilitation by a perceptual task

We replicated earlier studies showing that saccades to targets that also serve as targets for a perceptual task have shorter latencies (Bieg et al., 2012; Guyader et al., 2010; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). In addition, we have narrowed down the nature of this facilitation. We found no evidence that it is either influenced by information gain (Experiments 1 and 2) or by differential effects of fatigue or practice, with or without perceptual task. It is also not caused by global arousal, because it is spatially specific (Experiment 4; Montagnini & Chelazzi, 2005). As our stimuli were displayed long enough, we can also rule out explanations based purely on urgency (Montagnini & Chelazzi, 2005). This latter view would be consistent with the absence of a peak velocity difference.

The effect of higher peak velocities with a perceptual task at hand vanished when corrected for subtle differences in amplitude (Experiment 1). Compared to our and other findings (Bieg et al., 2012), the study by Montagnini and Chelazzi (2005) reported a strong increase in peak velocities by about 35°/s compared to without a discrimination task. However, their conditions did not only differ by the presence of the discrimination task but also by urgency, caused by the early and short presentation of the discrimination target. These divergent findings might point to the fact that saccade latency and peak velocity can be manipulated independently with peak velocity being more sensitive to changes in urgency. An alternative explanation would be that the oculomotor system adjusts latency and peak velocity sequentially to achieve an earlier foveation. In a first step, the oculomotor system might reduce response thresholds in order to achieve shorter latencies (Reddi & Carpenter, 2000) and only then in a second step adjust the motor command to achieve a higher velocity, and thus shorter saccade duration. This strategy would be adaptive, because changes in latency can be comparatively large compared to changes in saccade duration and because stronger motor commands go along with more motor noise and thus higher endpoint variability of the saccade (Harris & Wolpert, 1998).

Another likely cause for the facilitation of a perceptual task might be the general motivation to solve it. The absence of a modulation by information gain (Experiments 1 and 2) and the presence of a modulation by task probability (Experiment 3) might suggest that the facilitation by a perceptual task is primarily caused by such a motivational mechanism. Several studies showed that saccade latencies are sensitive to motivation using reward as a proxy for motivation (Milstein & Dorris, 2007; Takikawa et al., 2002). Motivation can also be manipulated by other means, for example, peak velocities are higher when the saccade target signals the upcoming presentation of a face (Xu-Wilson, Zee, & Shadmehr, 2009). In our task, discrepancies in motivation might have resulted from the visual feedback at the end of each trial. However, differences between task-related and mere target-elicited saccades remain even when controlled for feedback (Bieg et al., 2012). Moreover, when the motivation to solve a task was the only driving cause for this facilitation, then it should also be observed when the discrimination task is in any than the visual modality. However, this is not the case. In our last experiment (Experiment 5), we found no differences in saccade latencies when people had to discriminate auditory rather than visual information. This argues against sheer motivation as the only driving cause of this facilitation.

From our series of experiments, we conclude that the nature of this facilitation is not the motivation to solve a task per se, but the motivation to foveate task-relevant visual information for further processing. Due to the lifelong and overlearned experience that the fovea is the best retinal locus to solve a discrimination task, this earlier foveation seems to occur irrespective of whether it is useful or not.

*Keywords: saccade, information gain, value, task-relevance, perceptual task, peripheral vision, foveal vision, latency, reaction time, motivation*

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# Study II

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# Trans-saccadic integration of peripheral and foveal feature information is close to optimal

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**Due to the inhomogenous visual representation across the visual field, humans use peripheral vision to select objects of interest and foveate them by saccadic eye movements for further scrutiny. Thus, there is usually peripheral information available before and foveal information after a saccade. In this study we investigated the integration of information across saccades. We measured reliabilities—i.e., the inverse of variance—separately in a presaccadic peripheral and a postsaccadic foveal orientation-discrimination task. From this, we predicted trans-saccadic performance and compared it to observed values. We show that the integration of incongruent peripheral and foveal information is biased according to their relative reliabilities and that the reliability of the trans-saccadic information equals the sum of the peripheral and foveal reliabilities. Both results are consistent with and indistinguishable from statistically optimal integration according to the maximum-likelihood principle. Additionally, we tracked the gathering of information around the time of the saccade with high temporal precision by using a reverse correlation method. Information gathering starts to decline between 100 and 50 ms before saccade onset and recovers immediately after saccade offset. Altogether, these findings show that the human visual system can effectively use peripheral and foveal information about object features and that visual perception does not simply correspond to disconnected snapshots during each fixation.**

## Introduction

The human visual system comprises a large field of view and high spatial resolution with an inhomogeneous representation across the visual field: high-acuity vision in the fovea and low-resolution vision in the periphery. To exploit this architecture, objects are selected based on peripheral information and then foveated with saccadic eye movements for further inspection in natural tasks (for reviews, see Schütz, Braun, & Gegenfurtner, 2011; Tatler, Hayhoe, Land, & Ballard, 2011). As a result, there are usually two sources of visual information about an object: peripheral information before the saccade and foveal information after the saccade. The question now is, what happens to peripheral object information acquired before foveation? Theoretically, in the extreme case peripheral information is only processed in order to select future fixation positions, then neglected for object perception. In this case, vision would start anew with each fixation. In the other extreme, peripheral information is maintained across the saccade and integrated with foveal information in a statistically optimal manner. This is the long-standing question of trans-saccadic perception and integration (for reviews, see Irwin, 1996; De Graef & Verfaillie, 2002; Melcher & Colby, 2008; Mathôt & Theeuwes, 2011; Higgins & Rayner, 2015).

Trans-saccadic integration is far from trivial because of three reasons: First, peripheral information arrives earlier than foveal information and would have to be stored in memory. Depending on the level and type of memory, low-level features or an abstract representation (Irwin, 1991) might be maintained. Second, since early visual areas are retinotopically organized (Engel, Glover, & Wandell, 1997), saccades shift the receptive fields across the scene, and information would have to be transferred from peripheral neurons to foveal neurons. A potential mechanism could be predictive remapping, which leads to presaccadic activation from a stimulus that will be in the receptive field only after

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the saccade (Duhamel, Colby, & Goldberg, 1992). Thus, neurons with receptive fields at the fovea could already gather information from the saccade target before the saccade is actually executed. Third, visual processing differs in the peripheral and foveal visual field, which leads to differences not only in visual sensitivity (Rovamo, Virsu, & Näsänen, 1978; Makela, Whitaker, & Rovamo, 1993) but also in the appearance of visual stimuli between the periphery and the fovea (Davis, Yager, & Jones, 1987; McKeefry, Murray, & Parry, 2007; Valsecchi, Toscani, & Gegenfurtner, 2013). As a result, peripheral and foveal information need to be calibrated before they can be integrated.

At present there is contradictory evidence whether peripheral and foveal information are integrated across saccades. On one hand, several studies have found little evidence for integration (Bridgeman & Mayer, 1983; Rayner & Pollatsek, 1983). For instance, when different spatial patterns are shown at the same location before and after a saccade, subjects have problems fusing the two stimuli (Irwin, 1991). Several studies have also shown poor performance in the detection of trans-saccadic changes (Bridgeman, Hendry, & Stark, 1975; Henderson & Hollingworth, 1999), which often has been interpreted as evidence that peripheral information is not preserved across saccades and thus not integrated with foveal information. However, poor change detection could also be interpreted as a sign of integration, since a strong fusion of peripheral and foveal signals might restrict access to the separate signals (Hillis, Ernst, Banks, & Landy, 2002) and thereby raise the threshold to detect changes during the saccade. Along these lines, the locations of briefly flashed objects are integrated at the time of saccades (Cicchini, Binda, Burr, & Morrone, 2013).

On the other hand, some studies have shown evidence for integration. Peripheral preview can facilitate the recognition of objects (Pollatsek, Rayner, & Collins, 1984). When the contrast of peripheral and foveal stimuli is varied independently, this preview effect turns out to be larger for strong peripheral and weak foveal information (Demeyer, De Graef, Wagemans, & Verfaillie, 2009). Similarly, the color appearance of postsaccadic stimuli was biased in the direction of presaccadic information (Wittenberg, Bremmer, & Wachtler, 2008), and adding color noise to a presaccadic display biased trans-saccadic color perception towards postsaccadic information (Oostwoud Wijdenes, Marshall, & Bays, 2015). When the orientations of the peripheral and foveal object were varied independently, the distribution of perceived orientations was unimodal and located in between the peripheral and foveal stimulus orientations (Demeyer et al., 2010). While these studies suggest the involvement of peripheral information, they did not measure reliabilities and were not able to quantify the amount of peripheral information used. Thus, they leave open the question how the two sources of information are exactly integrated.

The integration of several perceptual signals is often studied within a Bayesian framework (for reviews, see Ernst & Bülthoff, 2004; Kersten, Mamassian, & Yuille, 2004). According to maximum-likelihood estimation, independent signals should be weighted by their relative reliabilities to achieve a statistically optimal integration. Previous research has found evidence for optimal integration within modalities (Jacobs, 1999; Hillis, Watt, Landy, & Banks, 2004) and across modalities (Ernst & Banks, 2002; Alais & Burr, 2004), as well as for dynamic changes over time (Wolpert, Ghahramani, & Jordan, 1995). Optimal integration of pre- and postsaccadic information has been reported for the perceived location of objects (Niemeier, Crawford, & Tweed, 2003) as well as for the location of reach targets (Vaziri, Diedrichsen, & Shadmehr, 2006). Object location, however is a special case, because to compute object location in external space, the retinal position of the object and an extraretinal signal about gaze direction have to be combined (Henriques, Klier, Smith, Lowy, & Crawford, 1998), even in the absence of eye movements. In addition, the execution of a saccade changes both of these components. This is different for other features—for example, orientation or color—because they can be computed from retinal signals alone. In this case, extraretinal signals would be necessary only for trans-saccadic integration, not for the computation of the features per se. As a result, it might be that these features are treated differently in trans-saccadic perception.

In this study we investigated whether peripheral and foveal feature information are integrated across saccades in a statistically optimal way. Therefore, we measured reliabilities of the presaccadic peripheral, the postsaccadic foveal, and the trans-saccadic percepts. Reliabilities are given by the inverse of the variance. The maximum-likelihood estimation makes two predictions with respect to the integrated signal. First, if peripheral and foveal information are incongruent, the trans-saccadic percept should be biased towards the more reliable information. Second, the reliability of the trans-saccadic percept should be higher than the reliability of peripheral and foveal information alone. We tested these predictions in Experiments 1 and 2. In Experiment 3 we tracked the weighting of peripheral and foveal information with high temporal resolution around the time of the saccade. In all of these experiments, we tested the natural scenario in which a peripheral object is foveated by a saccade; hence, presaccadic information was always peripheral, and postsaccadic information always foveal.

## Experiment 1: Biasing perception through presaccadic information

In this experiment we tested whether presaccadic peripheral information is maintained across the saccade and biases object perception in a way predicted by maximum-likelihood integration when there is a conflict between peripheral and foveal information. In order to do this, we measured peripheral and foveal reliabilities separately using two-alternative forced-choice orientation judgments. Based on these measurements, we predicted optimal peripheral weights. If both cues are integrated optimally, then peripheral and foveal information should be weighted according to their relative reliability (Equation 1). As contrast information is not maintained across the saccade (Melcher, 2005; Demeyer et al., 2009), we manipulated the foveal target contrast so that its reliability was either superior to the peripheral target, approximately equal, or inferior. We additionally measured perceptual responses with both peripheral and foveal information present. In this case, we introduced a conflict in order to measure the relative weight of peripheral and foveal information at different foveal reliabilities and then compared observed against predicted weights.

### Methods

#### *Participants*

Fourteen observers (12 women, two men, mean age = 24 years, range = 20–29) who were unaware of our goals participated in this experiment. Observers were students of the Justus Liebig University Giessen and were paid for participation. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee LEK FB06 at the university (proposal number 2013-0020). All observers gave informed consent and had normal or corrected-to-normal vision.

#### *Stimuli and setup*

Stimuli were plaid stimuli—i.e., a vertical and horizontal grating, both with a spatial frequency of 2 c/° overlaid by a Gaussian window with a standard deviation of 0.4° of visual angle. The overall contrast remained constant, as both individual contrasts added up to a fixed value of 0.4. Thus, a vertical contrast of 0.1 means that the horizontal contrast was 0.3. Here, we report the contrast of the vertical component only. Whereas the horizontal component was perfectly aligned to the cardinal axis, the orientation of the vertical component varied throughout the experiment. To measure peripheral and foveal performance separately in peripheral and foveal trials, stimuli were replaced by a Gaussian blob either after or before the saccade. The blob had the same size as the plaid and a peak contrast of 0.4.

Stimuli were displayed using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in MATLAB on a VIEWPixx monitor at a 1920 × 1080 pixel resolution and a 120-Hz refresh rate. The monitor had a size of 51.5 × 29 cm and was viewed at a distance of 48.5 cm. This resulted in 32 pixels/°. The luminance of black, gray, and white pixels was 0.23, 121, and 230 cd/m$^2$, respectively, and the output of the monitor was linearized. Eye movements of the right eye were recorded using the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002) and an EyeLink 1000 (SR Research Ltd., Ontario, Canada) with a sampling rate of 1000 Hz. Participant responses were recorded via a standard keyboard.

#### *Procedure*

In all trials, participants had to indicate whether the vertical component of a plaid stimulus was tilted clockwise (cw) or counterclockwise (ccw). A fixation cross in the screen center prompted participants to start the trial by pushing the space bar. After a random time between 0.75 and 1.5 s, the target appeared 15° left or right from screen center. The fixation cross was removed after an additional 200 ms (overlap paradigm). Targets switched as soon as the EyeLink detected that the eye exceeded a distance of 1.5° with respect to the screen center. This guaranteed that the target would be switched during the saccade, when vision is suppressed (for a review, see Ibbotson & Krekelberg, 2011). At the end of each trial, a bar appeared at the target location in one of two random orientations (cw or ccw). Participants could alternate between these two orientations pressing the plus key and selected their desired response with the Enter key. Afterwards, participants received visual feedback about their response.

In integration trials (Figure 1, left column), the foveal target was displayed for as long as the peripheral target in each trial. For instance, if it took 200 ms from target onset to target switch, the foveal target was presented for 200 ms as well. Thus the presentation duration depended on the eye-movement latency within each trial. This guaranteed that observers were provided with roughly the same amount of peripheral and foveal information within each trial. To guarantee that observers also had approximately the same viewing time across trials, they received feedback when the saccadic reaction time was too fast or too slow (target switch below 157.5 ms or above 257.5 ms). In these cases, a high or a low beeping sound was played and no visual feedback about the performance was

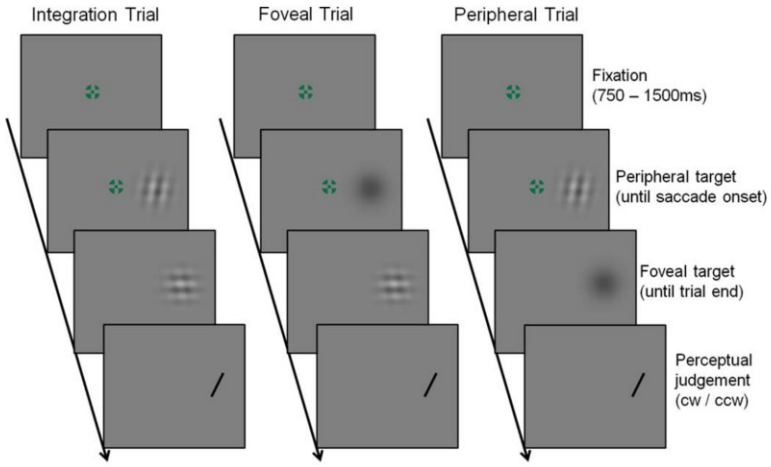


Figure 1. Trial procedure for peripheral, foveal, and integration trials. In all trials, a saccade target appeared at 15° eccentricity and had to be foveated. Afterward, observers had to decide whether the vertical component of the plaid was tilted cw or ccw. In peripheral trials (right column), plaid stimuli were visible only until saccade onset and were then replaced by a Gaussian blob during saccade execution. In foveal trials (middle column), the Gaussian blob was visible until saccade onset and was then replaced by the plaid stimulus. Foveal targets (single and integration trials) were displayed in one of three possible contrasts (fovea high, mid, or low), whereas the peripheral target was always displayed at high contrast. In integration trials (left column), the tilt of the peripheral target was shifted by 2.5° either cw or ccw (here the shift is exaggerated for demonstration purposes). Stimuli are not drawn to scale.

shown on the screen. Observers were told to keep their eye-movement latency within the given time window, as trials outside this time window were not considered for analysis.

To assure the same viewing time in single trials, peripheral and foveal targets were displayed for an individually fixed presentation duration. This duration was derived from the median individual latency in integration trials. Peripherally appearing plaid stimuli switched to a Gaussian blob after this time or if the eye exceeded the critical distance of 1.5°. In these cases, observers never had foveal information about the target (Figure 1, right column). Foveal targets switched from a Gaussian blob to a plaid stimulus during the saccade and were then displayed for the given presentation duration (Figure 1, middle column).

### Design

All participants started with the integration trials. In integration trials, the foveal contrast of the vertical component was either high (0.3), mid (0.1), or low (0.05), while the peripheral contrast was always high (0.3). Foveal orientations varied from −4° to +4° in eight steps (±0.5°, ±1°, ±2°, ±4°), with positive values indicating clockwise orientations. The orientation of the peripheral target was shifted either −2.5° or +2.5° with respect to the foveal target. We measured a psychometric function for every combination of foveal contrast and peripheral orientation shift. This resulted in 480 trials (3 foveal contrasts × 2 peripheral shift directions × 8 foveal orientations × 10 repetitions).

Peripheral and foveal trials were measured interleaved in the same session. For every observer, we measured four psychometric functions identical with the contrast levels in integration trials (three foveal contrasts, one peripheral contrast). Psychometric functions were sampled with 10 data points based on 16 observations each (±0.5°, ±1°, ±2°, ±4°, ±8°). This resulted in 640 trials (4 psychometric functions × 10 orientations × 16 repetitions).

### Data and eye-movement analysis

Saccade onsets were detected offline using the EyeLink 1000 algorithm. Saccade latencies were defined as the first saccadic frame with respect to target onset. To keep peripheral and foveal viewing time constant, integration trials in which the saccade was not detected in the given time window (157.5 to 257.5 ms) were excluded from further analysis. In total, we rejected 20% of trials (on average: 97 out of 480 trials).

Perceptual choices were converted into proportion cw responses for every stimulus orientation value, and a cumulative Gaussian was fitted to the data using psignifit 4.0 (Schütt, Harmeling, Macke, & Wichmann,

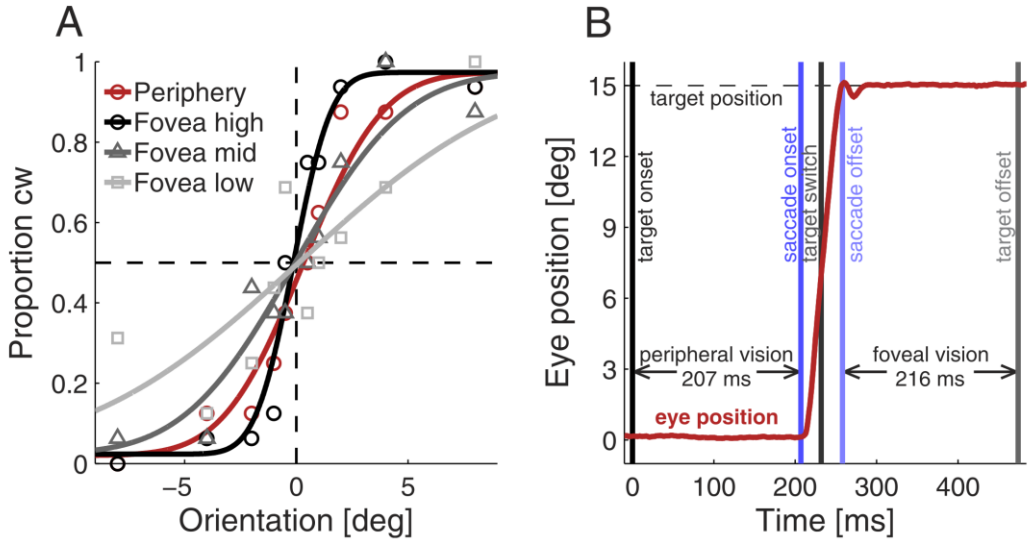


Figure 2. Manipulation of foveal reliability and gaze-contingent paradigm. (A) Proportion cw responses for different orientations with fitted psychometric functions in peripheral and foveal trials for one observer. Positive orientations denote a cw tilt. Foveal discrimination performance increases with increasing contrast (light gray to black). In peripheral trials (red), contrast was identical to the high-foveal-contrast condition. (B) Horizontal eye position over time for one trial. The target is switched during saccade execution, allowing comparable peripheral and foveal viewing time.

2015). Just-noticeable differences (JNDs) were defined as the standard deviation of the underlying Gaussian. The optimal peripheral weight (for a review, see Ernst & Bülthoff, 2004) is then given by

$$w_{per} = \frac{rel_{per}}{rel_{per} + rel_{fov}} \quad (1)$$

with

$$rel = \frac{1}{JND^2} \quad (2)$$

Results were compared using one-way repeated-measures ANOVAs and post hoc $t$-tests. If not noted otherwise, all $t$-tests were two-tailed and $p$-values were compared against a Bonferroni-corrected alpha level of 0.05.

## Results

To determine the extent to which the brain maintains peripheral information across saccades, we measured reliabilities for foveal and peripheral vision separately, as well as the bias of the trans-saccadic percept when peripheral and foveal information were set in conflict. The bias which presaccadic peripheral vision optimally exerts on the percept can be modeled using maximum-likelihood integration (Ernst & Banks, 2002).

For each observer in each condition, we varied the vertical orientation and fitted a cumulative Gaussian to the proportion of cw responses over the different orientations. Figure 2A shows psychometric functions for one observer for the periphery and the three different foveal contrast conditions. Our manipulation of foveal reliability was successful, as JNDs increased with decreasing foveal contrast from 1.1° (fovea high, $SD = 0.28°$) to 2.8° (fovea mid, $SD = 0.85°$) to 7.4° (fovea low, $SD = 2.14°$), $F(2, 26) = 105.50$, $p < 0.001$. JNDs in the fovea mid condition were significantly elevated compared to the fovea high condition, $t(13) = 9.89$, $p < 0.001$, and those in the fovea low condition were higher than in the fovea mid condition, $t(13) = 8.75$, $p < 0.001$. For peripheral vision, JNDs were 2.1° on average ($SD = 0.87°$). Based on these separately measured JNDs, we predicted optimal peripheral weights as in Equation 1.

To test these model predictions, we measured peripheral weights for the trans-saccadic percept. In integration trials, targets were switched during saccades (Figure 2B). Foveal contrast either remained high or was switched to mid or low. Additionally, peripheral information was misaligned by 2.5° in either direction. Consider that peripheral and foveal infor-

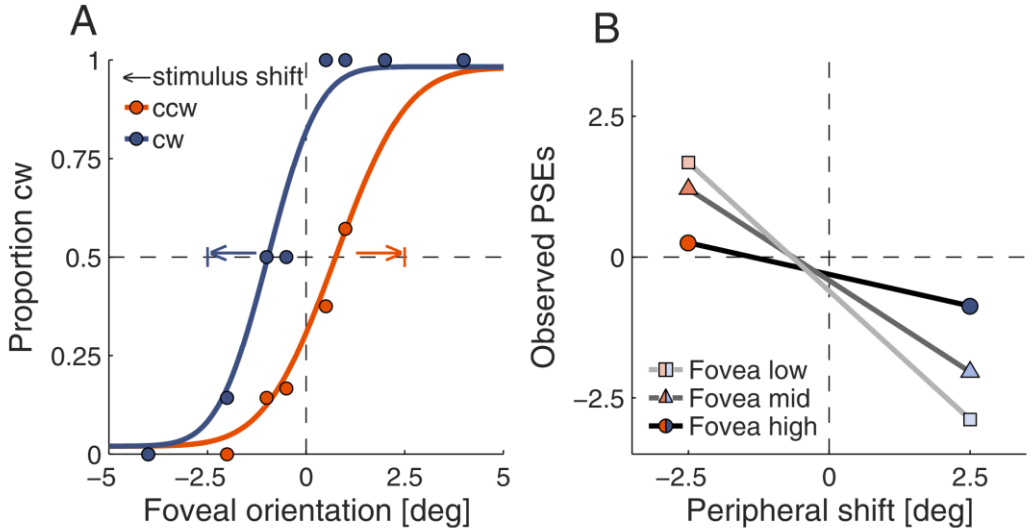


Figure 3. Experiment 1, calculation of peripheral bias. (A) Proportion cw responses and psychometric functions in integration trials (fovea high condition). One psychometric function is fitted for each peripheral orientation shift. The observed peripheral bias is calculated as the difference in PSE values between cw (blue curve) and ccw shift (orange curve) relative to manipulation. (B) PSE values for the two peripheral shifts and the three foveal contrast conditions relative to the peripheral-shift manipulation. Lines indicate regressions for each foveal contrast. Slopes ($\times -1$) correspond to the observed peripheral weight.

mation are integrated: If peripheral information is tilted ccw, it requires a cw foveal signal so that the trans-saccadic percept is perceived as being aligned with the cardinal vertical axis. As we computed functions over foveal contrasts, this corresponds to a shift of psychometric functions towards more clockwise values (Figure 3A, orange curve). The influence which is exerted by peripheral information can be measured by the difference between curves (Figure 3A, orange and blue curve) at the orientations which were judged equally often as cw and ccw (the point of subjective equality, PSE). If peripheral information has no influence on the percept (no integration), PSE values for the different peripheral shifts should be zero. If, however, perception is solely driven by peripheral information, PSE values should be –2.5° (cw shift) and +2.5° (ccw shift). Thus the difference of these two PSE values relative to the peripheral shift corresponds to the observed peripheral weight (Figure 3B).

As predicted by the model, the influence of peripheral information on the trans-saccadic percept increased with decreasing foveal reliability from 0.24 (fovea high, $SD = 0.13$) to 0.55 (fovea mid, $SD = 0.23$) to 0.83 (fovea low, $SD = 0.20$), $F(2, 26) = 48.95$, $p < 0.001$—low versus mid: $t(13) = 3.98$, $p = 0.002$; mid versus high: $t(13) = 5.4$, $p < 0.001$. A peripheral weight of 0 would indicate that peripheral information was ignored, whereas a weight of 1 would indicate that foveal information was ignored. All peripheral weights were statistically different from 0—fovea high: $t(13) = 7.08$, $p < 0.001$; mid: $t(13) = 8.97$, $p < 0.001$; low: $t(13) = 15.75$, $p < 0.001$—and from 1—fovea high: $t(13) = 22.45$, $p < 0.001$; mid: $t(13) = 7.3$, $p < 0.001$; low: $t(13) = 3.16$, $p = 0.008$—indicating that in all conditions, peripheral and foveal information were both considered and neither of them was ignored.

We predicted peripheral weights based on individual reliabilities from foveal and peripheral trials and compared observed against predicted weights (Figure 4). Observed weights coincided with predicted weights and did not differ significantly in any of the conditions (all $p$ values $> 0.1$). For 11 out of 14 observers, peripheral weights increased consistently with decreasing foveal contrast (Supplementary Figure S1). A possibility to quantify the agreement between data and model predictions over all foveal contrasts is to compute the best fitting line through the origin, based on the aggregated data. If model predictions and data perfectly match, this would result in a slope of 1. Here, this line had a slope of $b = 0.89$. Such a slope below 1 suggests that the foveal reliability was slightly overestimated relative to the peripheral reliability for the low- and the mid-foveal contrast condition.

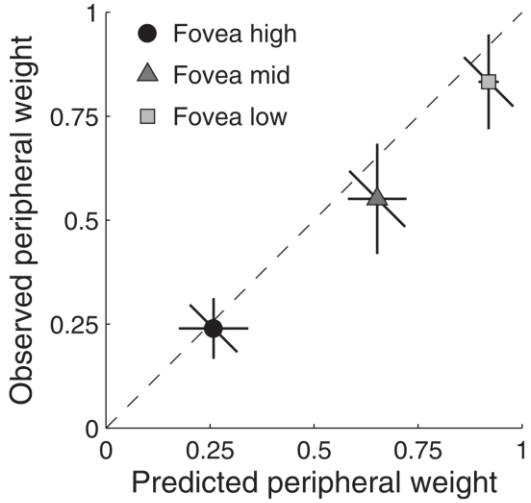


Figure 4. Experiment 1, observed against predicted peripheral weights for the three foveal contrast conditions. All error bars denote 95% confidence intervals. Diagonal error bars mark the error of the differences between observed and predicted values and have to be compared to the identity line. Observed weights on the identity line are statistically optimal. Performance below the line indicates an overweighting of foveal information, whereas performance above the identity line indicates an overweighting of the periphery. The slope of the best fitting line through the data and the origin is $b = 0.89$.

### Discussion

Here we investigated the extent to which peripheral object information acquired before the saccade is maintained after foveation and biases the trans-saccadic percept. Peripheral information clearly influenced the trans-saccadic percept. We found that the weight that was assigned to peripheral information increased with a higher relative reliability of peripheral vision. Under normal viewing conditions, when no contrast manipulation was introduced between peripheral and foveal vision, peripheral weights were optimal. When foveal contrast and thus the reliability of foveal vision was reduced, peripheral weights were also not different from optimal but showed a slight overweighting of the fovea. In everyday life, foveal vision has a far better resolution than peripheral vision. This tendency towards suboptimality for lowered foveal contrasts thus might reflect an internal prior of the visual system that foveal vision is superior to peripheral vision.

Showing that presaccadic information biases trans-saccadic perception of object features and that the strength of this bias is modulated by the relative reliability of the pre- and postsaccadic signal (Demeyer et al., 2009; Oostwoud Wijdenes et al., 2015) can only be seen as a first hint for (optimal) integration. Neither of the aforementioned studies measured the reliabilities for the pre- and postsaccadic displays separately, and they were thus not able to compare the bias on the trans-saccadic percept to the benchmark of maximum-likelihood integration and draw conclusions regarding the efficiency of the peripheral preview effect. But even after showing that the bias of presaccadic peripheral vision on the trans-saccadic percept behaves in a manner that is statistically close to optimal, we cannot yet conclude that information is actually integrated across saccades. Optimal weights only indicate that the information is used in an optimal manner. Any bias, optimal or not, can also be explained with probabilistic cue switching (e.g., Nardini, Jones, Bedford, & Braddick, 2008; Serwe, Drewing, & Trommershäuser, 2009), where people stochastically alternate between the two cues without integrating them. To overcome this limitation and rule out the possibility of cue switching, we performed a second experiment, where the precision of a congruent trans-saccadic signal was measured and compared to the optimal prediction.

## Experiment 2: Reliability of the trans-saccadic percept

To show that peripheral and foveal information are actually integrated across saccades and that the bias shown in Experiment 1 is not due to cue switching, we measured the foveal and peripheral reliabilities separately and predicted the JND of the trans-saccadic percept that would result from statistically optimal cue integration. As the congruency between two cues has been shown to be essential for integration (Atkins, Fiser, & Jacobs, 2001; Parise, Spence, & Ernst, 2012), conflicts between cues could disrupt optimal integration. We therefore decided to assess the predictions of the JND of the trans-saccadic percept in a separate experiment, where peripheral and foveal orientations were always identical.

### Methods

For the reliability experiment, we measured 14 observers (11 women, three men, mean age = 23 years, range = 19–29) who were unaware of the aims of the experiment, three of whom had already taken part in Experiment 1. They all gave informed consent, were paid for participation, and had normal vision.

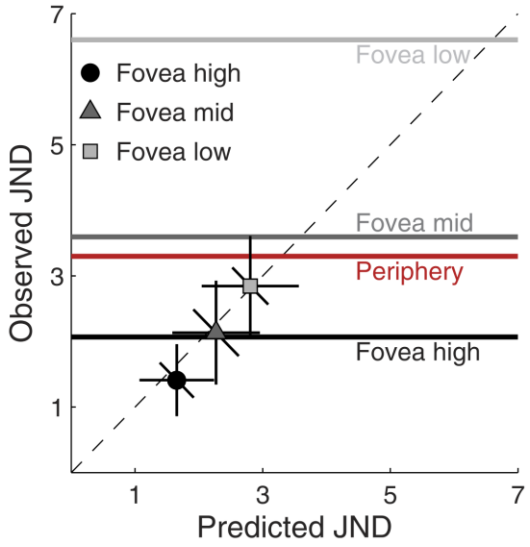


Figure 5. Experiment 2, observed against predicted JNDs averaged across observers, with error bars denoting 95% confidence intervals. Diagonal error bars mark the error of the differences between observed and predicted values and have to be compared to the identity line. Lines indicate the average JND in single trials. JNDs on the identity line are statistically optimal. Values above the identity line indicate suboptimal behavior. The slope of the best fitting line through the data and the origin is $b = 0.96$.

Stimuli, setup, and trial procedure were identical with the first experiment, with the exception that the order of single and integration trials was now counterbalanced across participants. Therefore, participants were given auditory feedback in all trials whenever their eye movement in reaction to the target was not in a given time window (target switch below 137.5 ms or above 297.5 ms). Beforehand, all observers completed a training session that consisted of 180 integration trials in a separate session.

In integration trials, the orientation of the vertical component varied in 10 steps from −4° to +4° (±0.25°, ±0.5°, ±1°, ±2°, ±4°). No peripheral shift was introduced this time, and the peripheral and foveal targets were thus always in line with respect to their orientation. Again, we measured performance for the same three foveal target contrasts (0.3, 0.1, 0.05) while the peripheral contrast was constant (0.3). This resulted in 480 trials (3 foveal contrasts × 10 orientations × 16 repetitions). In peripheral and foveal trials, we included orientation values of −8° and +8°. The single-trial session thus consisted of 768 trials (4 psychometric functions × 12 orientations × 16 repetitions).

One observer was not susceptible to our contrast manipulation in single trials. JNDs for the three different foveal contrast conditions were all above 6°, with the worst performance in the high-foveal-contrast condition (7.4°). We did not include data from this participant for further analysis. Also, we excluded trials in which the saccade did not take place in the given time window. This applied to 7.8% of integration trials (on average: 37 out of 480 trials removed) and 8.9% of single trials (on average: 69 out of 768 trials removed).

If two independent cues are integrated, then the reliability of the integrated percept ($rel_{int}$) is the sum of the two individual reliabilities (for a review, see Ernst & Bülthoff, 2004):

$$rel_{int} = rel_{per} + rel_{fov} \quad (3)$$

The peripheral ($rel_{per}$) and foveal ($rel_{fov}$) reliabilities are given by Equation 2. The predicted JND of the integrated percept can then be derived by adjusting Equation 2:

$$JND_{int} = \sqrt{\frac{1}{rel_{int}}} \quad (4)$$

## Results

Identical to Experiment 1, we measured the peripheral reliability as well as the foveal reliability for three different contrasts. Again, our manipulation of foveal reliability was successful, as JNDs increased with decreasing foveal contrast from 2.07° (fovea high, $SD = 1.25°$) to 3.6° (fovea mid, $SD = 1.5°$) to 6.6° (fovea low, $SD = 1.1°$), $F(2,24) = 104.07$, $p < 0.001$. JNDs in the fovea mid condition were significantly higher than in the fovea high condition, $t(12) = 6.72$, $p < 0.001$, and those in the fovea low condition were significantly higher than in the fovea mid condition, $t(12) = 7.99$, $p < 0.001$. JNDs derived from peripheral trials were 3.3° ($SD = 1.83°$) on average. Based on these JNDs, we predicted performance in integration trials (Equations 3 and 4) and compared predicted against observed performance.

JNDs in integration trials also increased with decreasing foveal contrast from 1.41° (fovea high, $SD = 0.91°$) to 2.13° (fovea mid, $SD = 1.31°$) to 2.85° (fovea low, $SD = 1.26°$), $F(2, 24) = 14.39$, $p < 0.001$—mid versus high: $t(12) = 2.96$, $p = 0.012$; low versus mid: $t(12) = 2.88$, $p = 0.014$. Predicted and observed values highly coincided and did not differ significantly from each other (Figure 5; all $p$ values $> 0.3$). To quantify the agreement between observed JNDs and model predictions, we fitted a line through the origin based on

the aggregated data points. If predicted and observed values across all conditions perfectly matched, this line would fall on the identity line (slope of $b = 1$). Here, the best fitting line had a slope of $b = 0.96$.

A strong model prediction to test integration is that the integrated percept should be more reliable than each of the single cues. This can be tested by comparing whether JNDs from integration trials are lower than the smaller of the two single JNDs. For each of the three contrast conditions, we tested separately whether JNDs in the trans-saccadic percept were lower than in the better of the two single conditions (one-sided $t$ tests). This was true for the fovea high condition, where no contrast or any other manipulation between peripheral and foveal target was introduced, $t(12) = 1.78$, $p = 0.05$. In this condition, 11 out of 13 observers showed better performance than with either foveal or peripheral vision alone (Supplementary Figure S2). The same effect was observed in the fovea mid condition, $t(12) = 1.82$, $p = 0.047$. Here, nine out of 13 observers showed a benefit. In the fovea low condition, eight out of 13 observers had a lower JND than with either foveal or peripheral vision alone. This condition failed to show significance, $t(12) = 1.32$, $p = 0.105$.

### Discussion

In this experiment, we tested the second prediction of maximum-likelihood estimation to show that peripheral and foveal information is integrated across saccades. If information is integrated, then the reliability of the trans-saccadic percept should be the sum of the two single reliabilities and thus greater than the reliability of either peripheral or foveal vision on their own. For the high and mid foveal contrasts, JNDs from integration trials were significantly lower than the better of either the peripheral or foveal JNDs. For the low foveal contrast, no significant benefit of integration was observed. For all foveal contrasts, observed performance could be well predicted by optimal integration. This is strong evidence that information is integrated optimally across saccades.

In terms of reliability, the benefit of integrating two signals is highest when they are both equally reliable. If they differ strongly, the integrated percept will be very similar to the more reliable of the two signals. Consequently, the effect size for the conditions in which peripheral vision is either inferior (high foveal contrast) or superior (low foveal contrast) should be comparatively low. Although the failure to show a significant decrease in JNDs for the low foveal contrast is in line with the tendency of suboptimal weights for decreased foveal contrasts in Experiment 1, it can also be explained by a lack of statistical power and does not necessarily speak against integration—especially because in this contrast condition, observed values perfectly matched predictions from statistical optimal behavior. Most importantly, despite any issues of statistical power, we could find evidence for integration even in the high-foveal-contrast condition. In this condition, the target was continuously displayed without any manipulation in either contrast or orientation and thus corresponds to normal vision, where objects do not change during the saccade.

In a previous study, the aspect ratio of ellipses was varied independently before and after the saccade (Demeyer et al., 2010). That study also reported a bias in perception according to the peripheral information but did not observe a reduction in the variability of responses. However, in those experiments, trials with congruent and incongruent peripheral and foveal information were interleaved. It might be that integration is impaired with increasing probability and magnitude of incongruence between peripheral and foveal information, since a high correlation between cues seems to be a requirement for integration (Atkins et al., 2001; Parise et al., 2012). Here we provide evidence that information is integrated very close to optimally when no conflict between peripheral and foveal vision is introduced.

## Experiment 3: The time course of trans-saccadic integration

So far, we have shown that information about objects acquired before and after saccades is integrated according to its relative reliability. However, vision is a very dynamic process, and splitting it up into a presaccadic peripheral and postsaccadic foveal component does not yet tell us much about the exact time course of trans-saccadic information accrual. Specifically for presaccadically obtained information, opposite predictions can be derived from the literature: On the one hand, peripheral information acquired shortly before saccade onset might contribute most to the trans-saccadic percept because attention is enhanced (Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011) and crowding is reduced (Harrison, Mattingley, & Remington, 2013) at the saccade target prior to the onset of the movement. These results predict a continuously rising weight towards saccade onsets. On the other hand, there are findings and mechanisms which would suggest a reduced contribution of information immediately prior to saccade onset. First, due to delays in neural transmission, information which is available up to 80 ms prior to saccade onset does not modify the upcoming saccade (Becker & Jürgens, 1979; Caspi, Beutter, & Eckstein, 2004;

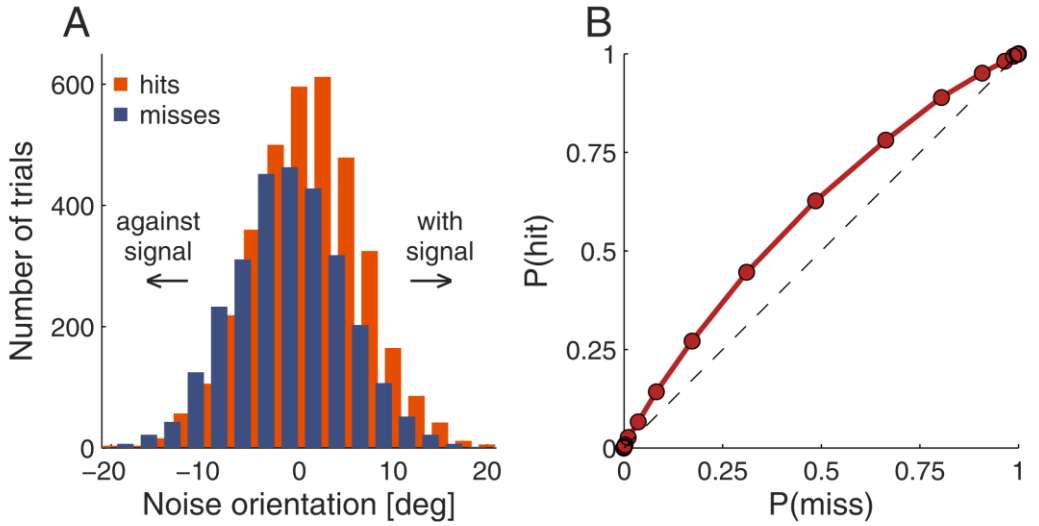


Figure 6. Experiment 3, ROC analysis. (A) Histogram of noise distributions for foveal vision (fovea high) 15 ms after saccade offset. Trials were split up into hits and misses and then compared using an ROC analysis. Evaluation criteria for the histograms are slightly offset for better visibility. (B) ROC curve for the displayed distributions. For 20 linearly spaced criteria along the distributions, we compared the proportion of hits against the proportion of misses exceeding these criteria. Here, the AUC is 0.6.

Ludwig, Gilchrist, McSorley, & Baddeley, 2005; Ludwig, Davies, & Eckstein, 2014). This interval is called the "saccadic dead time." Second, visual information starts to be suppressed up to 100 ms before an eye movement, and suppression is strongest around saccade onset (Diamond, Ross, & Morrone, 2000; Schütz et al., 2007; Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009; Dorr & Bex, 2013). Both saccadic dead time and saccadic suppression predict a decrease in information gathering before saccade onset. To resolve this issue, we measured trans-saccadic perception with a reverse noise-correlation experiment.

Reverse correlation (for a review, see Murray, 2011) is a method that allows for a very fine-grained temporal resolution of this time course. The logic is as follows: Throughout one trial, the target's orientation signal is not constant, but corrupted by dynamically changing noise. If any particular time point is contributing to the final percept, then perceptual responses and the orientation noise at this time point should be related.

## Methods

For the reverse-correlation experiment, we recorded data from four participants (all women, mean age = 25 years, range = 24–26). All four observers also participated in Experiment 1. They all gave informed consent, were paid for participation, and had normal vision.

Trial procedure was identical to the integration trials in the first two experiments, except that no overlap paradigm was used and the true target orientation (signal) was corrupted by noise which changed every 25 ms. Again, the contrast of the vertical component was high (0.3) for peripheral targets and either remained constant (fovea high) or was reduced to 0.05 (fovea low) during the saccade. Importantly, the true underlying signal was negligibly small, with the noise determining most of the actual orientation. Although only the noise is relevant for the analysis, we included an underlying target signal so that performance would be slightly above chance. This was meant to keep observers involved with the task while maintaining the balance between hits and misses. The orientation signal was $\pm 0.5°$, $\pm 1°$ for the fovea low condition and $\pm 0.25°$, $\pm 0.5°$ for the fovea high, corrupted by noise with zero mean and a standard deviation of $\sigma = 6°$. Observers performed 1,600 trials in each of the two foveal contrast conditions. We had to discard 320 trials in the fovea high condition due to technical issues. Performance was 0.56 and 0.58, respectively, for the high and low foveal contrast conditions. For all observers in all conditions, the proportion of a correct response (hit) was between 0.5 and 0.6. Different contrast conditions were recorded in different sessions,

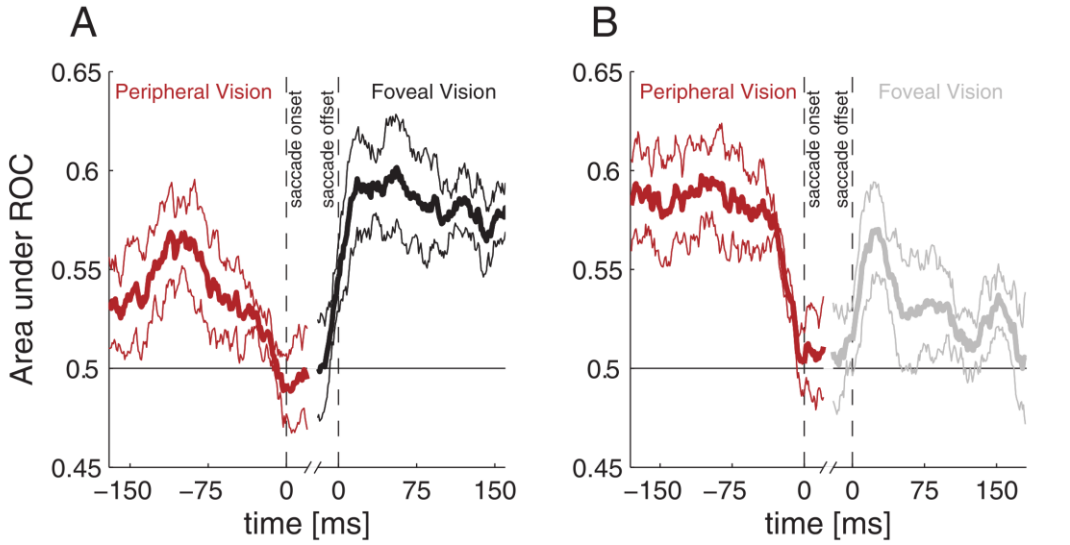


Figure 7. Experiment 3, AUC time course for the fovea high (A) and the fovea low (B) condition. Black, gray, and red lines are the AUCs derived from an ROC analysis based on trials aggregated over all four observers. Thin lines correspond to the 95% confidence interval of between-subjects variability.

and the order of the conditions was balanced across observers.

Noise values from every trial were time logged to saccade onset for peripheral vision and to saccade offset for foveal vision. As saccades have different durations, it is not possible to determine a continuous graph throughout the saccade. However, we completed the analysis for the first 20 ms after onset and the last 20 ms prior to saccade offset. Noise values were recoded so that positive values coincided with the true underlying signal, then split up into hits and misses (Figure 6A). Then noise distributions for every millisecond were compared using receiver operating characteristic (ROC) analysis (Ludwig et al., 2014). If a given time point exerts no influence on the trans-saccadic percept, then the noise value at this time point does not influence the perceptual decision, and thus the two distributions of noise values for hits and misses are not distinguishable. If, however, a given time point exerts a high influence on the trans-saccadic percept, then a strong positive noise value should increase the likelihood of a correct response, whereas a noise value in the opposite direction would bias the response in favor of a false answer. The noise distribution for hits and misses should thus be easy to distinguish. The discriminability of two distributions can be measured using an ROC analysis. If two distributions are identical, the area under the ROC curve (AUC) is 0.5. If the two distributions are perfectly apart (no overlap), the area under the ROC curve is 1.

To determine ROC curves, we computed the proportion of hits against the proportion of misses which exceeded given criteria (Figure 6B). Criteria were linearly spaced in 20 steps between the maximum and the minimum noise values. Then we determined the area under this ROC curve. The AUC corresponds to the influence this time point exerts on the trans-saccadic percept. This procedure was repeated for every millisecond. Alternatively, instead of using an ROC analysis, the two noise distributions can be averaged and their difference plotted as a function of time. As both procedures produced comparable results, we chose to use the ROC analysis, because it considers the whole noise distributions and not just their mean value.

To determine saccade offsets offline, we fitted a linear regression to the eye position at every time point, with a time window of 11 ms. Offsets were defined as the first frame when the slope of the linear regression fell below 150°/s.

## Results

Using a reverse-correlation technique, we measured for each point in time how much that point contributes to the trans-saccadic percept. Here the contribution of each time point is expressed as AUC, the area under the

ROC curve (Figure 6). Whenever the AUC is above 0.5 (chance level), information at this time point biases the trans-saccadic percept, with higher AUC values denoting a higher contribution. Please note that the AUC values are only informative within their specific time course, and should not be compared across different conditions.

In both conditions, the peripheral AUC is above 0.5 (Figure 7), showing that peripheral vision in general contributes to the trans-saccadic percept. The relative contribution of peripheral vision is higher in the low- than in the high-foveal-contrast condition. Common to both conditions is the decrease starting between 100 and 50 ms prior to the saccade until a value of 0.5 is reached at saccade onset.

After saccade onset, the AUC remains constant around chance performance. This indicates that right after saccade onset, no (or only little) information is considered for perception. Prior to saccade offset, it rapidly increases and is instantly elevated as the eye lands at its target location. This increase is more pronounced in the fovea high condition (Figure 7A), where the AUC remains relatively constant throughout foveal vision. In the fovea low condition, performance is very dissimilar across participants, as can be judged from the confidence interval. Across participants, we can observe a postsaccadic enhancement after saccade offset, followed by a decrease starting 25 ms after the saccade and an oscillation between accuracy values of 0.51 and 0.54. However, a strong postsaccadic enhancement is observed in only one of the observers (Supplementary Figure S3).

## Discussion

Here we outlined the time course of trans-saccadic information gathering using a reverse noise-correlation approach. Consistent with Experiments 1 and 2, the individual contributions of peripheral and foveal vision to the integrated percept are modulated by their relative reliability. We also show that information gathering starts to decrease between 100 and 50 ms prior to the saccade and is lowest around saccade onset. Then, already before saccade offset, it increases, resulting in elevated foveal processing right at the end of the saccade. This can be observed especially under normal viewing conditions, when peripheral and foveal contrast were identical.

Reverse-correlation allows for fine-grained temporal resolution, but the method has its limitations: AUC values are only informative within their specific time course, and absolute values should not be compared across conditions. There are also large interindividual differences in the time courses, which makes it difficult to make precise judgments about the timing of effects. This is why we want to highlight properties which are common in the pooled data (Figure 7) and across participants (Supplementary Figure S3). These are that performance is above chance for peripheral vision, it dips around the time of the saccade, and AUC values are instantly elevated after saccade offset.

### *Decrease of information gathering before saccade onset*

The gathering of information declined well before saccade onset. With respect to the underlying cause of this decline, it is important to note that AUC values indicate the weighting of information; hence we cannot distinguish whether no sensory information is taken in or whether it is taken in but not used. In the following we will discuss the relationship of this decline to other phenomena of peri-saccadic perception: saccadic suppression, presaccadic attention shifts, and saccadic dead time.

The time course outlined here shares some similarities with peri-saccadic contrast sensitivity. Consistent with our results, saccadic suppression precedes a saccade by 50–100 ms and has its maximum around saccade onset (Diamond et al., 2000; Schütz et al., 2007; Dorr & Bex, 2013). But whereas suppression usually outlives the saccade by up to 50 ms, information gathering was immediately restored after saccade offset. Thus, the trans-saccadic time course outlined here cannot be fully explained by saccadic suppression.

Previous research on the coupling of attention and eye movements has shown that attention is shifted towards the saccade target prior to the saccade, leading to a continuous rise of identification performance at the saccade target until saccade onset (Deubel & Schneider, 1996; Rolfs et al., 2011). This attentional modulation is exactly opposite to our decline of information gathering before saccade onset. There are three major methodological differences between our paradigm and the attention paradigms that might explain this discrepancy. First, while we used a target with low visual contrast, which might be very susceptible to saccadic suppression of contrast sensitivity, attention studies typically use high-contrast stimuli, which might be less susceptible to suppression (Rolfs et al., 2011). Second, several target locations have to be monitored at the same time in attention paradigms, while there was only one target location in our paradigm. Possibly the attentional benefit at the saccade target is only evident if attention has to be split among several locations. Third, studies on attention typically mask the target stimulus. If saccadic suppression reduces the efficacy of target and mask at the same time, these effects might cancel each other out, such that no effort of saccadic suppression is observable.

Alternatively, the decay of peripheral information gathering prior to saccade onset could be related to the

saccadic dead time (Becker & Jürgens, 1979; Caspi et al., 2004; Ludwig et al., 2005; Ludwig et al., 2014), during which incoming information does not influence saccade target selection anymore. Of course, target selection cannot be altered during the time of saccade motor programming, but it is not completely evident why the processing of object features should be interrupted by the programming of the saccade.

The observed time course could also be interpreted as a sacrifice of peripheral information for foveal information. Peripheral information gathering could decline before the saccade such that foveal information can be used immediately when the eyes land on the target. In fact, the weighting of foveal information was already above chance at saccade offset, and it might be that this instantly elevated weighting is only possible if peripheral information briefly before saccade onset is neglected. This effect might not be specific for stimulus transitions from periphery to fovea, because instantly elevated processing after a saccade has also been observed for targets which were in the periphery after the saccade but had been foveated during the previous fixation (Ludwig et al., 2014).

#### *Increase of information gathering before saccade offset*

Information gathering increased already before saccade offset and was instantly elevated at saccade offset. We think that this finding does not necessarily mean that information was actually gathered during the saccade, but that the rise in AUC before saccade offset could instead be caused by our experimental methods. Although we analyzed the data on a millisecond basis, the temporal resolution is inevitably limited by the frequency of noise changes in the experiment. Since the noise changed only every 25 ms, the data of each millisecond analysis interval are not independent of each other. Thus, despite the high temporal resolution in the analysis, we cannot reliably map sudden changes in performance like they might be observed around saccade offset (Figure 7A). Let us imagine a binomial process where information processing is completely turned off during the saccade and immediately switched on as the eye lands: Because the ROC analysis is computed for each millisecond but noise values are not independent on a millisecond basis, orientations right before saccade offset can be identical to orientations after offset. This overlap depends on the timing of the saccade offset relative to the updating of the noise value. As a consequence, the ROC analysis would yield values above chance even during the saccade. Hence the time window of 25 ms is too long to perfectly map this sudden switch, and would have resulted in a continuous increase even before the switch takes place. In the case of our results, this means that our time course is a low-pass-filtered version of the true underlying process and that the steep increase in information gathering at the end of the saccade could be even steeper and starting at a later time point. Regardless of the exact starting point of this increase, information gathering was immediately enhanced after saccade offset. To rule out the possibility that this instantly elevated performance is only due to the way the saccade offset is determined, we chose a criterion which provided us with a very early offset (Methods section; see also Figure 2B).

## General discussion

In this study we asked whether presaccadic peripheral information is maintained across saccades and integrated with postsaccadic foveal information in a statistically optimal manner. We measured peripheral and foveal orientation discrimination separately and then tested two predictions of maximum-likelihood estimation: When peripheral and foveal information was incongruent, peripheral information biased the trans-saccadic percept to an extent predicted by maximum-likelihood estimation (Experiment 1). By integrating congruent peripheral and foveal information, discrimination performance benefited in terms of reliability (Experiment 2). Moreover, we tracked the trans-saccadic time course and showed that information gathering starts to decrease well before the saccade, reaches a minimum at saccade onset, and is instantly elevated at saccade offset (Experiment 3).

Across Experiments 1 and 2, optimal integration almost perfectly predicted the values observed. Neither any of the peripheral weights (Experiment 1) nor any of the JNDs (Experiment 2) were different from optimality. Thus the visual system is able to integrate information across saccades in a (nearly) optimal manner. In our experiments, conditions were chosen to facilitate integration by several factors. First, we varied foveal contrast to achieve comparable peripheral and foveal reliabilities. Since foveal vision is highly superior to peripheral vision for most tasks and features (for a review, see Strasburger, Rentschler, & Jüttner, 2011), the benefit of integration might be too small to be measured reliably under normal conditions. Second, there was only one object on the screen; and third, this object was the target for both the eye movement and the perceptual task. It might be that integration falls short of optimality for other conditions. Under the present conditions, however, peripheral and foveal information are integrated in a nearly optimal manner. Such an optimal integration requires three capacities: the maintenance of peripheral information from the pre- to the postsaccadic interval, the transfer to foveal neurons, and the calibration of peripheral and foveal

information to overcome differences in processing across the visual field.

A recent approach that could account for the *calibration* process highlights the importance of visual feature prediction and sensorimotor learning. Several studies have shown that trans-saccadic changes in object features (Cox, Meier, Oertelt, & DiCarlo, 2005; Li & DiCarlo, 2008) and associations between saccade direction and postsaccadic foveal displays (Bompas & O'Regan, 2006) can be learned. Moreover, the postsaccadic foveal appearance of a target is predicted based on presaccadic peripheral information (Herwig & Schneider, 2014; Weiß, Schneider, & Herwig, 2014). Such a prediction mechanism would be helpful in overcoming differences in resolution as well as biases across the visual field and creating visual stability. Of course, a comparison of presaccadic peripheral and postsaccadic foveal information is a necessary requirement for learning new associations between periphery and fovea.

If integration relies on some sort of capacity-limited *memory* (Prime, Tsotsos, Keith, & Crawford, 2007; Bays & Husain, 2008), then integration should be impaired by the presence of other objects, as is the case in cluttered scenes. Previous research has shown that visuospatial attention is shifted towards the saccade target prior to the execution of the saccade (Kowler et al., 1995; Deubel & Schneider, 1996; Rolfs et al., 2011). It is possible that this shift of attention is necessary to preserve and transfer presaccadic information. In this case, integration of information about other objects in the periphery should be reduced and fall short of optimality. In line with this hypothesis, it has been shown that changes in natural scenes are more likely to be detected if they are close to the saccade landing position (Henderson & Hollingworth, 1999), and that saccades suppress processing at nontarget locations (Khan, Blohm, Pisella, & Munoz, 2015). These circumstances might also explain why previous studies in which the saccade and the perceptual target were not identical failed to detect integration of pre- and postsaccadic information (O'Regan & Lévy-Schoen, 1983; Irwin, 1991).

One potential candidate for the *transfer* across space is spatial predictive remapping (Duhamel et al., 1992; Kusunoki & Goldberg, 2003), which describes the finding that neurons respond before a saccade to stimuli that will be in their receptive field only after the saccade. These findings have been interpreted in two ways: It could be that receptive fields are actually shifted (Duhamel et al., 1992), or it could be that only information is transferred from the future location of the receptive field (Cavanagh, Hunt, Afraz, & Rolfs, 2010). The former would limit integration to a brief period of time before the saccade, because predictive remapping occurs only 50 ms prior to a saccade (Kusunoki & Goldberg, 2003) and because information could only be taken into account once the receptive field was remapped. The finding of Experiment 3 that peripheral information is accounted from −200 ms until shortly before saccade onset cannot solely be explained by the shift of receptive fields, because peripheral information is used already before remapping takes place. Hence, it supports the transfer-of-information view, which suggests that information is accumulated continuously in peripheral neurons and then transferred to foveal neurons. This view is also supported by the presence of remapped responses prior to a saccade to stimuli which were briefly flashed and already disappeared at the time of remapping (Umeno & Goldberg, 2001).

Our study provides the first evidence that information about object *features* can be integrated optimally across saccades. Using computational modeling, it has been shown that several perceptual phenomena reflect optimal integration of pre-, peri- and postsaccadic information about object *location* (Niemeier et al., 2003). As mentioned in the Introduction, location is a special feature because it is essential to eye movements and because extraretinal signals are necessary to compute location. This is not the case for other object features like orientation, color, and so on. Here we could show that peripheral information is used not only for the calculation of location but also for identification of purely perceptual features like orientation.

The fact that foveal information is processed immediately after the offset of the saccade is a new and quite surprising finding. The predictive remapping (Duhamel et al., 1992) and the presaccadic shift of attention (Kowler et al., 1995; Deubel & Schneider, 1996) to the saccade target might allow this early processing of foveal information. Ecologically, it is also a sign of optimal behavior because it allows minimization of fixation durations and sampling of more locations in the visual surround. Such optimal processing of peripheral and foveal information is important for many tasks. Eye movements in visual search have been shown to be similar to an ideal searcher that maximizes information gain with each fixation (Najemnik & Geisler, 2005). This requires a representation of the visibility of the search target at different eccentricities and a memory of how much information has been gathered at different locations in the search area. An optimal integration of peripheral and foveal information across saccades would maximize the extraction of information and could be an important aspect in optimizing visual search performance. In addition, uncertainty about visual objects is available not only for optimal gaze guidance—which is a rather automatic process most of the time—but also for decision making when subjects have to choose the stimulus with lower uncertainty (Barthelmé & Ma-

massian, 2010). Understanding the mechanisms and limitations of trans-saccadic perception is a key factor towards a better insight into more complex processes like visual search and perceptual decision making.

## Conclusions

The present work shows that the visual system can store and integrate purely perceptual information across saccades with an efficiency that is indistinguishable from optimality. It helps to understand how our brains are able to create a stable perceptual world despite the drastically varying sensory input. Visual perception thus does not correspond to disconnected snapshots during each fixation but rather to an assembled, integrated stream of information.

*Keywords:* trans-saccadic perception, optimal integration, maximum-likelihood estimation, peripheral vision, foveal vision

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**Study III**

# The necessity to choose causes the effects of reward on saccade preparation

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## Abstract

When humans have to choose between different options, they can maximize their payoff by choosing the option that yields the highest reward. Information about reward is not only used to optimize decisions but also for movement preparation to minimize reaction times to rewarded targets. Here, we show that this is especially true in contexts in which participants additionally have to choose between different options. We probed eye movement preparation by measuring saccade latencies to differently rewarded single targets (single-trial) appearing left or right from fixation. In choice-trials, both targets were displayed and participants were free to decide for one target to receive the corresponding reward. In blocks without choice-trials, single-trial latencies were not or only weakly affected by reward. With choice-trials present, the influence of reward increased with the proportion and difficulty of choices and decreased when a cue indicated that no choice will be necessary. Choices caused a delay in subsequent single-trial responses to the non-chosen option. Taken together, our results suggest that reward affects saccade preparation mainly when the outcome is uncertain and depends on the participants' behavior, for instance when they have to choose between targets differing in reward.


## Introduction

Humans frequently decide where to look next. We shift our gaze 2-3 times a second by saccadic eye movements, each time choosing a different region or object of the visual scene for high acuity processing. This qualifies the oculomotor system as a suitable candidate to study decision-making in humans and other primates (Glimcher, 2003; Gold & Shadlen, 2007). The selection of a particular target over others as well as the time required to initiate an eye movement (latency) are both informative about the underlying decision process.

Saccade latencies are not only influenced by low-level stimulus features (Schütz, Braun, & Gegenfurtner, 2011; Tatler, Hayhoe, Land, & Ballard, 2011), but also by motivational factors like reward: Monkeys initiate saccades earlier and with higher peak-velocities when they expect a reward compared to non-rewarded saccades and reduced latencies are preceded by a modulated discharge rate of neurons in several brain areas (Kawagoe, Takikawa, & Hikosaka, 1998; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Sato & Hikosaka, 2002; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002; Ikeda & Hikosaka, 2003). To maximize outcome in decision-making, an option's expected value (EV), the combination of reward magnitude and probability,

has to be considered. Indeed, neural activity in the lateral intraparietal area (LIP) covaries with both reward magnitude and probability (Platt & Glimcher, 1999). In humans, EV scales with activity of frontal areas (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Rolls, McCabe, & Redoute, 2008; Barkley-Levenson & Galván, 2014).

Despite this clear neurophysiological evidence that brain activity scales with reward, there are contradictory findings about its influence on eye movement preparation. Some studies did not find effects on saccade latencies in monkeys (Leon & Shadlen, 1999; Platt & Glimcher, 1999) or reported changes in peak-velocity rather than latency when investing the effect of reward in humans (Chen et al., 2014; Reppert et al., 2015). However, there is also evidence favoring a modulation by reward. Two studies (Milstein & Dorris, 2007, 2011) investigated whether saccades are influenced by a target's EV. They showed that when two targets were presented (two-target trial), humans (Milstein & Dorris, 2007) and monkeys (Milstein & Dorris, 2011) more frequently chose the highly rewarded target. When one target was presented (single-target trial), latencies were affected by reward magnitude, but showed a stronger linear relationship with EV. This led to the conclusion that a representation of EV is incorporated in saccade preparation.

Where might these contradictory findings come from? A specific feature of the studies reporting an influence of EV on saccade preparation (Milstein & Dorris, 2007, 2011) was the combined recording of several different trial types in the same experiment. Whereas latency analyses were based on responses to single-targets, additional trials were recorded in which participants had to choose among two targets (two-target trials) or trials with a distractor flashed before onset of the saccade target (distractor trials). These different trial types might have interacted: there is ample evidence that inter-trial priming can affect saccade metrics, especially when a competition between several targets is involved (Bichot & Schall, 2002; Kumada & Humphreys, 2002; Belopolsky & van der Stigchel, 2013).

Here, we investigated the hypothesis that effects of reward on saccade preparation are modulated or caused by interleaved choices between multiple targets. We measured saccade preparation by means of saccade latencies to single-targets (single-trials) and varied the proportion of interleaved choices (choice-trials) in a block. It is important to note that choice-trials were only included as independent variable: All results are based on latencies in single-trials. Differences in latencies to less and highly rewarded targets were present in blocks with interleaved choices – and mostly absent in blocks where participants never made a choice. The magnitude of this effect

increased with increasing proportion and difficulty of choices. Choices caused a delay in subsequent saccade responses to the non-chosen target. Modelling latency distributions suggested that this delay was due to a reduced baseline level in the response signal.

## Results

### Increased latency differences between less and highly rewarded targets

In Experiment 1, we tested the hypothesis that saccade preparation in response to rewarded single-targets is modulated by the presence of choices which participants have to make in a block. To this end, we measured single-trial saccade latencies (Fig 1a) in blocks without choice-trials (0%) or in blocks with different proportions of choice-trials randomly interleaved (25%, 75%). In single-trials, one target appeared at 15° eccentricity either left or right from fixation. Participants had to saccade to the target within 500 ms to receive the reward. In choice-trials, both targets were displayed and participants were free to decide for one target to obtain the corresponding reward. In every block, each hemifield was assigned either a highly or a less rewarded target. Across blocks, the difference in reward magnitude between the opposite hemifields could be either small (4 vs 6) or large (1 vs 9).

Saccade latencies from single-trials are shown in Figure 1b. With an increasing proportion of choice-trials (0%, 25%, 75%) latency differences between less and highly rewarded targets increased for the large (2, 29 and 52 ms) and small reward difference (8, 22 and 45 ms), $F(2,48) = 49$, $p < 0.001$ (interaction proportion choice-trials × reward magnitude). This was mainly because latencies to less rewarded targets increased linearly with an increasing proportion of choice-trials, $F(1,24) = 83.86$, $p < 0.001$. Without choice-trials, latencies between less and highly rewarded targets did not differ significantly for the large reward difference: $t(24) = 0.43$, $p = 0.671$, but they did for the small if not Bonferroni-corrected: $t(24) = 2.12$, $p = 0.045$ ($\alpha' = 0.05/6$ [3 proportion choice-trials × 2 reward differences] = 0.0083). The corresponding Bayes factor (BF) favored the null hypothesis (i.e. reward does not influence latencies) for the large, $BF = 0.23$, but there was no conclusive evidence for the small reward difference, $BF = 1.38$. With 25% choice-trials, however, latency differences were significantly larger than without choice-trials, large: $t(24) = 6.76$, $p < 0.001$, small: $t(24) = 4.02$, $p < 0.001$. Compared to 25%, latency differences were even more pronounced with 75% choice-trials for the small reward difference, $t(24) = 3.29$, $p = 0.003$, but

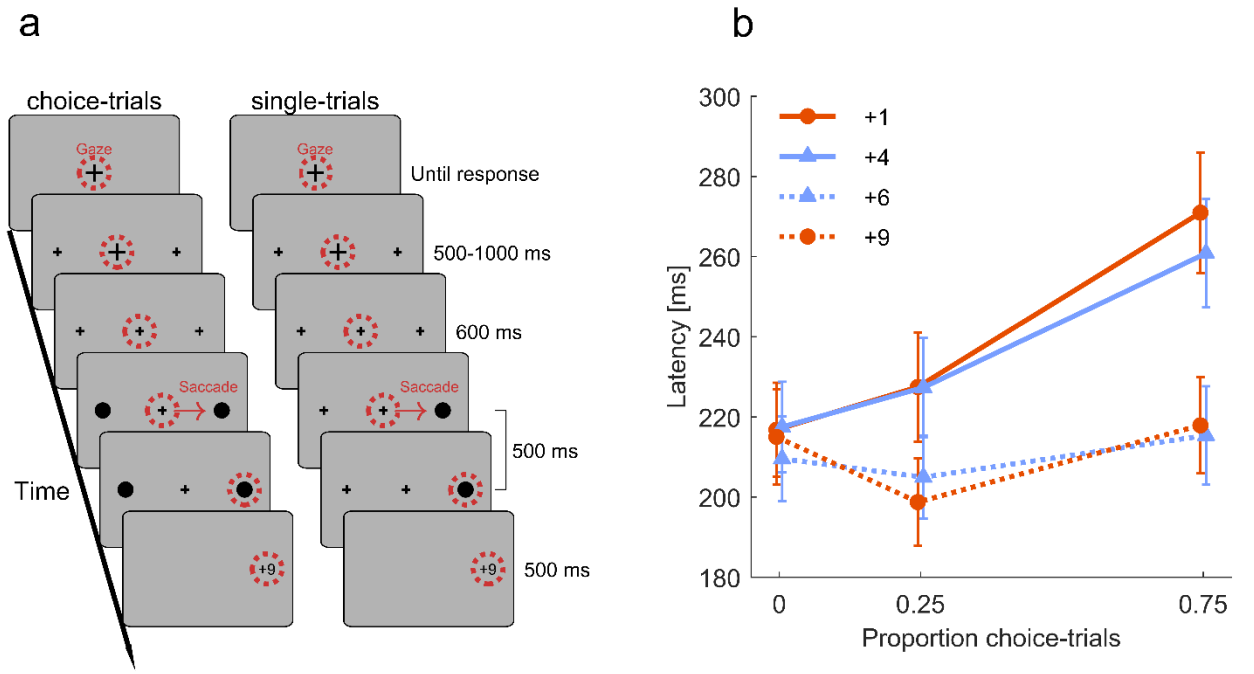


**Figure 1**. **The effect of choice- on single-trials**. ***a***, Trial procedure for choice- (left column) and single-trials (right column). Participants started trials by fixating the cross at the screen center (red dashed circle, not shown in the experiment) and simultaneously pressing a button on a keyboard. Two placeholders appeared in the periphery and after a random interval, the central fixation cross changed its size to indicate the onset of the target(s) in 600 ms. In single-trials, one target (black dot) replaced one of the two placeholder crosses and was displayed for 500 ms. Participants received a reward if they saccaded to the target during its presentation. In choice-trials, both placeholders turned into dots and participants could choose which target to saccade to in order to obtain the corresponding reward. Each side was either assigned a highly or a less rewarded target and participants were informed about the distribution of rewards before starting each block. ***b***, Latency in single-trials as a function of the proportion of choice-trials in the same block. Dashed lines refer to the highly rewarded, solid lines to the less rewarded targets. Blue colors and triangles denote the small, orange colors and circles the large reward difference. Error bars are 95% confidence intervals. Values are offset horizontally for better visibility.

failed to reach significance for the large reward difference, $t(24) = 2.29$, $p = 0.031$, $BF = 1.88$. We found no evidence for an effect of reward difference (all $ps > 0.4$).

In Experiment 1, we mainly found differences in saccade latencies between less and highly rewarded targets when choices were interleaved. Because participants consistently chose highly rewarded targets, this observation could arise due to the choices themselves or because higher choice-trial proportions also implied lower saccade frequencies to the less rewarded (i.e. non-chosen) target. In Experiment 2, we eliminated this imbalance in saccade frequency by altering the

frequency of single-trials to each target so that participants moved equally often to both targets if they always chose the highly rewarded target in choice-trials. Even with equated saccade frequency, participants still showed longer latencies to less rewarded single-targets, that is, non-chosen targets, $F(1,7) = 123.97$, $p < 0.001$ (Fig. 2a; main effect reward magnitude). Latency differences were 29 ms for the large, $t(7) = 6.30$, $p < 0.001$, and 17 ms for the small reward difference, $t(7) = 4.27$, $p = 0.004$, and thus similar to Experiment 1. Like in Experiment 1, we did not find evidence that reward differences affected latencies (all $ps > 0.1$).

We compared latency differences from Experiment 2 and the 25% choice-trial condition in Experiment 1. Experiments are identical with regard to choice-trial probability, but differ in saccade frequency. A 2×2 ANOVA with the factors reward difference (within) and experiment (between) revealed no significant main effect of experiment, $F(1,31) = 0.39$, $p = 0.565$, $BF = 0.31$. In a similar ANOVA, we compared latency differences from Experiment 2 with the 0% choice-trial condition in Experiment 1. Here, conditions from both experiments include the same saccade frequency, but differ with respect to choice-trial probability. Latency differences were larger in Experiment 2, $F(1,31) = 24.61$, $p < 0.001$, $BF = 29.72$. This suggests that latency differences between less and highly rewarded single-targets in blocks with interleaved choices occur even when overall saccade frequencies are matched for both targets.

To examine whether choices modulated the reward effects on saccade preparation or whether they caused them, we performed Experiment 3 where choice- and single-trial rewards were either incongruent or congruent, or where choice-trials were absent. In the congruent condition, highly rewarded targets for single- and choice-trials were presented in the same hemifield (equivalent to Experiment 1), whereas in the incongruent condition highly rewarded single- and choice-trials targets were presented in opposite hemifields. If the presence of choice-trials caused latency differences in single-trials, then single-trial latencies should only depend on which target is preferred in choice-trials and should be independent of the actual single-trial reward. Figure 2b shows mean and individual latencies for the different congruency conditions. Without choice-trials, latencies in both reward conditions perfectly coincided (196 ms) and did not differ significantly, $t(7) = 0.06$, $p = 0.956$, but the corresponding BF did not provide conclusive evidence, $BF = 0.37$. Instead, the effect of reward depended on the level of congruency, $F(2,14) = 21.54$, $p < 0.001$ (interaction reward magnitude × congruency). With congruent choice-trials present, latencies to less rewarded single-targets were increased by 29 ms (SD = 13 ms), $t(7) = 6.2$, $p < 0.001$. This

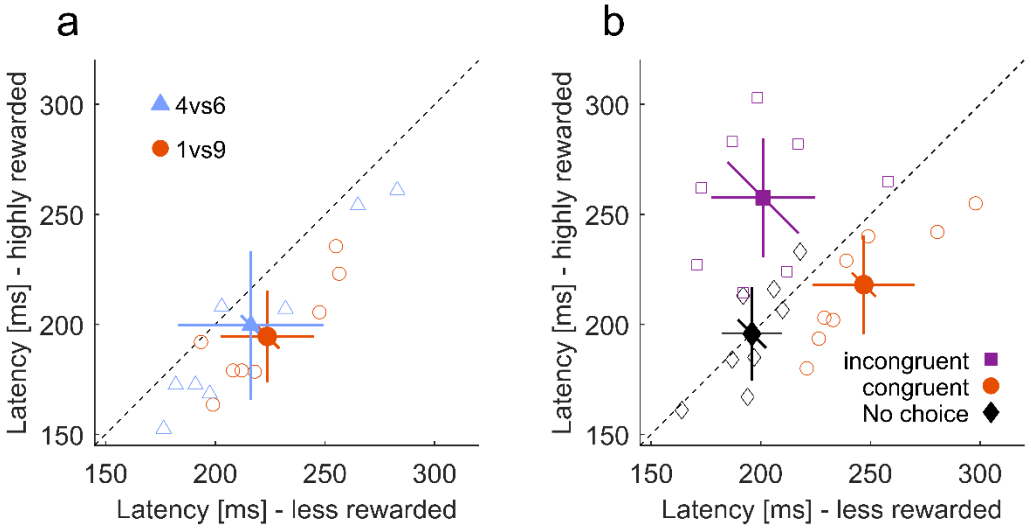


**Figure 2**. **Latency delays are caused by choice-trials**. ***a***, Results of Experiment 2. Single-trial latency for the highly versus less rewarded target when saccade frequency is equated for both hemifields. Open markers denote individual data and filled markers denote the mean with 95% confidence intervals. Diagonal error bars represent the error of the differences between high and low reward and have to be compared to the identity line. ***b***, Results of Experiment 3. Single-trial latency towards the highly compared to the less rewarded target when the reward in choice-trials was congruent (orange circle), incongruent (purple square) or without choice-trials (black diamond).

pattern was reversed with incongruent choice-trials (M = -57 ms, SD = 39 ms), $t(7) = 4.11$, $p = 0.005$. Increased latencies in single-trials thus did not depend on single-trial reward itself, but on reward in choice-trials and therefore on which target was chosen. It thus seems that choices caused rather than modulated, the observed reward effects in single-trials.

**The non-chosen target is inhibited in the subsequent single-trial**

Confronted with a choice, one could either increase saccade preparation towards the highly rewarded and thus chosen target or one could inhibit the less rewarded and thus non-chosen target (or any combination of more mechanisms, see discussion). The former case predicts lower latencies when highly rewarded single-trials follow a choice-trial, whereas the latter case predicts increased latencies when less rewarded single-trials follow a choice-trial. The latter case appears more likely, given that we mainly found increased latencies for the non-chosen target. To test whether inter-trial effects contributed to our results, we reanalyzed the 25% choice-trial condition of Experiment

1 with regard to previous trial effects. We compared single-trials following a choice-trial with single-trials following a single-trial (Fig 3). After choice-trials, saccades were initiated later when the upcoming trial was a single-trial to the non-chosen target, $F(1,24) = 11.82$, $p = 0.002$ (main effect reward magnitude). This cannot be attributed to a change in saccade direction, because there is no such difference when a previous single-trial was directed in the other or in the same direction, $F(1,24) < 0.01$, $p = 0.954$. An ANOVA which included both trial sequences, revealed an interaction of trial sequence with reward magnitude, $F(1,24) = 7.13$, $p = 0.013$ (i.e., an interaction of the black and red line in Figure 3). Thus, in single-trials with less rewarded targets of either *1*, $t(24) = 4.77$, $p < 0.001$, or *4* points, $t(24) = 3.98$, $p < 0.001$, saccades were significantly slower after a choice-trial. This suggests that the non-chosen target is inhibited in choice-trials, affecting the subsequent single-trial. We found no evidence that this effect increased with reward difference, $F(1,24) = 4.01$, $p = 0.057$.

**Adaptive inhibition of the non-chosen target**

Is the delay of saccades to the non-chosen target an adaptive behavior? If yes, then it should scale with the necessity to inhibit the less rewarded target in choice-trials. One possibility to manipulate the necessity for inhibition would be to change the relative salience of both choice targets. When the less rewarded target has a higher contrast than the highly rewarded one, stronger inhibition is required to make an optimal saccade and thus obtain the high reward. Any location-based inhibition should then propagate to single-trials and lead to larger latency differences. The opposite pattern should be observed when the highly rewarded target is more salient. A second possibility to manipulate the required inhibition would be cueing the upcoming trial type. If participants know that the next trial will be a single-trial, they can refrain from maintaining inhibition and rely on a purely visually evoked saccade instead. This, however, would require that the inhibition could be modulated by top-down control. We tested these two possibilities in Experiment 4 and 5.

In Experiment 4, we aimed to assess whether single-trial latency differences increase with the difficulty to saccade to highly rewarded targets in choice-trials. To this end, we changed the contrast of both choice-trial targets so that the contrast of the highly rewarded target was lower (difficult condition), higher (easy condition) or identical (medium condition). Beforehand, we

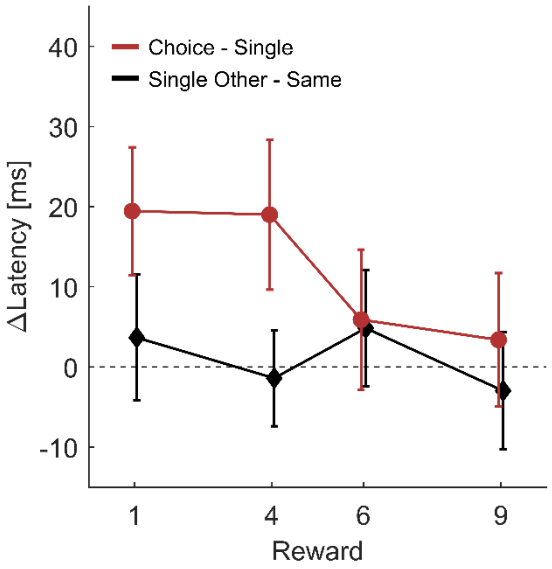


**Figure 3**. **Inhibition of the non-chosen target**. N-1 effects from Experiment 1. The difference in single-trial latency when the previous trial was a choice- compared to a single-trial (red circles). After a choice-trial, latencies to less rewarded single-targets, thus to the non-chosen target, are increased. This cannot be attributed to a change in saccade direction, because no such delay occurs when the previous trial was a single-trial in the opposite versus the same direction (black diamonds).

measured two control conditions as a manipulation check (Fig 4a). First, in the choice control task, participants had to choose one out of two targets which were either identical or different in contrast without receiving a reward. The probability of choosing targets on the right was lowest, when left targets had higher contrasts (M = 0.21, SD = 0.17), it was around chance when both contrasts were identical (M = 0.47, SD = 0.09) and highest when right targets had higher contrasts (M = 0.74, SD = 0.23), $\chi^2(2) = 12.17$, $p = 0.002$. Second, in the latency control task, we measured latencies to single-targets of different contrasts. Latencies decreased from 229 ms (low contrast) over 200 ms (medium contrast) to 196 ms (high contrast), $F(2,22) = 15.91$, $p < 0.001$. Compared to medium contrasts, latencies were increased for lower contrasts, $t(11) = 4.7$, $p = 0.001$, but they were not significantly decreased for high contrasts, $t(11) = 0.81$, $p = 0.433$.

Figure 4b shows individual and mean latencies for less and highly rewarded targets and for the three difficulty levels. Again, we found higher latencies to less rewarded targets, $F(1,11) = 23.22$, $p = 0.001$. Latency differences between less and highly rewarded targets were modulated by difficulty, $F(2,22) = 7.24$, $p = 0.011$. Compared to medium difficulty, latency differences were increased for the difficult condition, $t(11) = 2.23$, $p = 0.047$, and decreased for the easy condition,

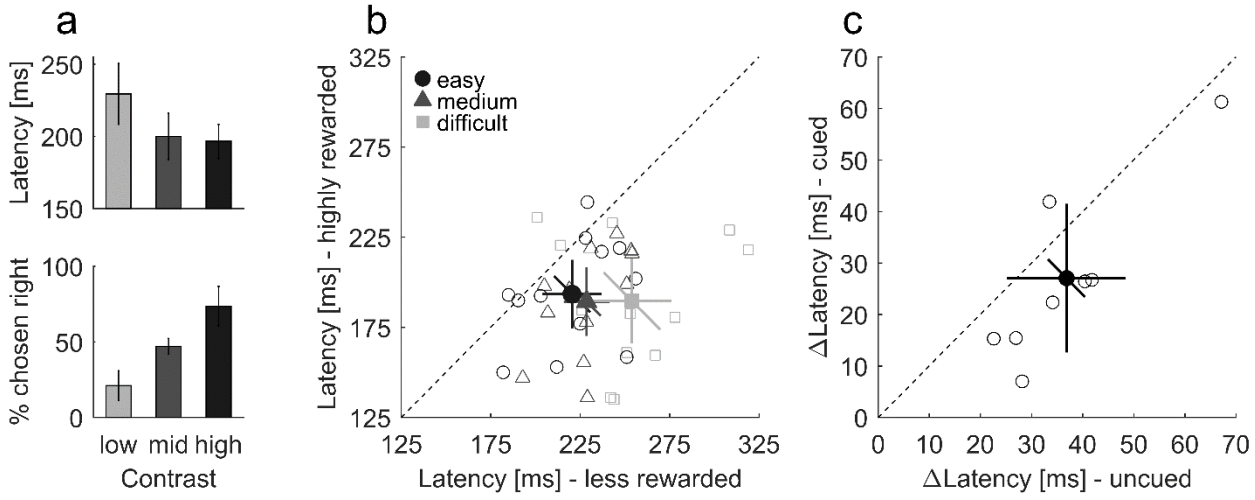


**Figure 4**. **Adaptive inhibition of the non-chosen target**. ***a***, Control latency task (top panel) and control choice task (lower panel) of Experiment 4. With increasing target contrast, latency in single-trials decreased and the target with the higher contrast was preferably chosen in choice-trials. ***b***, Latency to the highly versus the less rewarded target for the different levels of difficulty (Experiment 4). The difference in single-trial latency increased with increasing difficulty in choice-trials. ***c***, Results of cueing (Experiment 5). Latency differences between less and highly rewarded single-trials were reduced when single-trials were cued compared to uncued.

$t(11) = 2.35$, $p = 0.038$. Two separate ANOVAs suggested that difficulty affected latencies to less rewarded targets, $F(2,22) = 8.39$, $p = 0.002$, but not to highly rewarded targets, $F(2,22) = 0.29$, $p = 0.751$, $BF = 0.2$. Moreover, the probability to miss less rewarded single-trials increased with choice-trial difficulty, from 5% (easy), over 8.6% (medium) to 23.3% (difficult), $\chi^2(2) = 15.2$, $p = 0.001$. Misses were either due to too late (42.2%), too early (22.6%) or wrong saccades (35.2%). There was only one missed trial (<0.1%) in highly rewarded single-trials.

To test whether this behavior is not only adaptive with regard to low-level stimulus features, but also with regard to top-down processes, we cued half of the single-trials in Experiment 5. If there is a contribution from a top-down component, for example a preparation for an upcoming choice-trial, then differences in single-trial latencies between the chosen and non-chosen targets should be reduced by cueing. Figure 4c shows differences in saccade latencies, for cued compared to uncued single-trials. Latency differences were 37 ms without and 27 ms with cue. Wilcoxon signed-rank tests revealed that the latency difference was above 0 in both conditions, $Z = -2.52$, $p = 0.012$, but reduced by the presence of a cue, $Z = -2.1$, $p = 0.036$. This indicates that there is a voluntary component contributing to the observation of delayed saccades, yet it cannot fully

account for it. In sum, the delay reduction by cueing (Experiment 5) and the delay increase with increasing difficulty (Experiment 4) point out that the inhibition of the non-chosen target is an adaptive behavior influenced by top-down and bottom-up factors.

**Decreased baseline level for the non-chosen target in single-trials**

In order to identify likely neural mechanisms which can explain the delay of saccades to single-targets due to interleaved choices, we recorded the whole latency distribution for two participants (Experiment 6) and fitted the LATER model (Carpenter & Williams, 1995; Noorani & Carpenter, 2016) to the single-trial data. The LATER model is helpful in pointing out potential neural mechanisms of motor responses and decision making, on the basis of reaction time distributions. It assumes that for every response (here single-trial saccade) at stimulus onset, evidence is accumulated starting from a baseline level $\theta_0$ with an average rate of rise $\mu$ until a response threshold $\theta_T$ is reached. Within one trial the accumulation rate rises constantly but varies across trials with a Gaussian standard deviation $\sigma$. Several studies identified such evidence accumulation in the primate brain (Hanes & Schall, 1996; Dorris & Munoz, 1998) that can account for saccade latency distributions. With behavioral data however, it is only possible to obtain information about the threshold height, that is, the difference between baseline level and response threshold, $\theta = \theta_T - \theta_0$. Since there is physiological evidence that the baseline firing rate in saccade related areas represents economic decision variables as reward and target probability (Dorris & Munoz, 1998; Platt & Glimcher, 1999) and saccades are initiated once the neural activity reaches a constant threshold (Hanes & Schall, 1996), we fixed the response threshold to an arbitrary value. The three remaining parameters are the baseline level, $\theta_0$, the accumulation rate, $\mu$, and its variability, $\sigma$.

To find out which of these three parameters can most likely explain the latency differences between conditions, we abided by the following procedure: For every individual, we applied a bootstrap procedure with 100 iterations. For every iteration, we fitted three versions of the model in which we allowed one of the parameters to vary across conditions while the remaining two were kept identical across conditions. We then used information weights (Burnham & Anderson, 2002), derived from the Bayesian information criterion (BIC) to compare the three model versions and thus to identify which parameter is best in explaining the latency differences across conditions. Information weights can range from 0 to 1 and higher values speak in favor of a particular model.

With regard to average latencies, we replicated our main findings also with the more extensive measurements with these two participants: Without interleaved choices, average single-trial latencies were M = 192 ms for the less and M = 187 ms for the highly rewarded target. With choice-trials present, latencies were M = 192 ms for the highly and M = 228 ms for the less rewarded target. For both participants, information weights (Fig 5a) were highest for the $\theta_o$ parameter (baseline level). Thus, changes in $\theta_o$ were best in explaining differences in latency distributions between conditions. Cumulative probability plots of latency distributions together with model fits are plotted in Figure 5b. Without choice-trials, baseline levels for less rewarded single-trials were reduced by 12 and 17% relative to baseline levels for highly-rewarded targets. With choice-trials present, baseline levels were reduced by 82% (Fig 5c) for both participants. Technically, this suggests that either a lower baseline level, an increased response threshold or both are most likely to explain delayed saccades to non-chosen targets.

## Discussion

In this study we investigated whether saccade preparation to single-targets is influenced by interleaved choices among two targets differing in reward and if this is able to account for differential previous results on the modulation of saccade latencies by reward. In blocks without choices (Experiment 1 and 3), we only found a comparatively small effect of reward on saccade latencies that was only significant in one (only without correction for multiple testing) out of three cases. When choices were present, reactions to less rewarded single-targets were delayed and the magnitude of this delay increased significantly with the proportion of choice-trials, both for saccades (Fig. 1b) and button presses (Heuer, Wolf, Schütz, & Schubö, 2017). When changing the reward congruency between choice- and single-trials, latency differences in single-trials depended on the reward assignments in choice- rather than in single-trials (Fig. 2b). Moreover, latency differences were adaptive because they scaled with the necessity to inhibit saccades which do not maximize reward during choices (Fig. 4b) and decreased when upcoming single-trials were cued in advance (Fig. 4c), suggesting the contribution of both, bottom-up and top-down factors. Increased latencies to less rewarded single-targets can be explained in terms of a reduced baseline level (Fig. 5). Although a difference in response threshold could technically also account for the observed latency difference, this is unlikely given that saccades are executed at a constant threshold (Hanes & Schall, 1996).

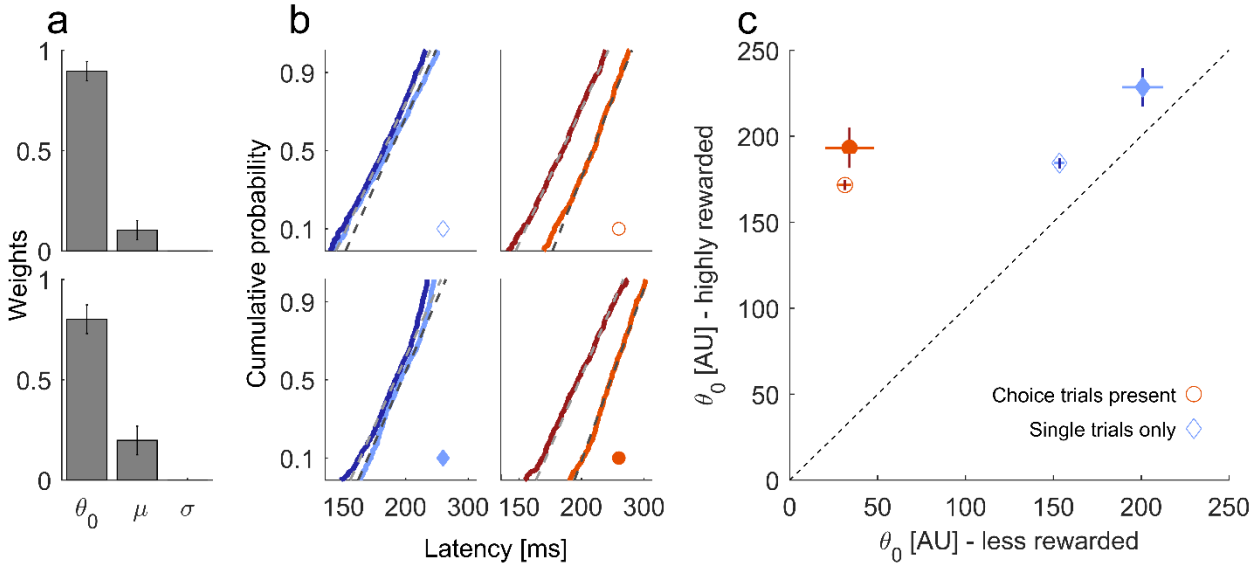


**Figure 5**. **Results from the LATER model**. ***a***, information weights for the different model fits when each of the three parameters was allowed to differ across conditions. Values represent the mean weight with 95% confidence intervals across 100 Bootstrap samples. Each row (consistent with **b**) represents a different participant. For both participants, the $\theta_0$ parameter, baseline level, was best in describing differences across conditions. ***b***, Reciprobit plots of single-trial latency distributions to the highly (dark colors) and the less rewarded target (brighter colors) when choice-trials were present (right column; orange/red colors) or absent (left column; blue colors). Each row represents a different participant. Dashed lines are model fits for the high (bright gray) and low reward (dark gray). Dots indicate which marker is used to plot the $\theta_0$ parameters in **c.** ***c***, Scatterplot of baseline levels, $\theta_0$, for the different conditions obtained by the model fit. Values represent the mean with 95% confidence intervals across 100 Bootstrap samples. Participants can be told apart by open or filled symbols (same as in **b**). With choice-trials present (orange circles), baseline levels for less rewarded single-trial targets were strongly reduced.

Taken together, our results suggest that information about reward might not always be incorporated for the preparedness of motor responses like saccadic eye movements. This does neither suggest that it is not represented in the brain, nor that it does not affect behavior. Rather, it suggests that reward affects preparation of saccades mostly when it is behaviorally relevant as in choice-trials and less so when it is behaviorally irrelevant as in single-trials. When responding to single-targets without strong temporal urgency, there is no necessity to optimize behavior, for instance, by preferring one target location over the other. Thus, the modulation of latencies in single-trials appears to be a direct effect of target selection and mostly no (or only an indirect) effect of reward per se.

Many studies have shown that reward influences oculomotor behavior. Monetary and non-monetary reward alters eye movement behavior, by changing saccade latencies (Lauwereyns et al., 2002; Itoh et al., 2003; Watanabe, Lauwereyns, & Hikosaka, 2003; Dunne, Ellison, & Smith, 2015), kinematics (Xu-Wilson, Zee, & Shadmehr, 2009; Hickey & van Zoest, 2012; Chen et al., 2014) and target selection (Markowitz, Wong, Gray, & Pesaran, 2011; Schütz, Trommershäuser, & Gegenfurtner, 2012; Failing, Nissens, Pearson, Le Pelley, & Theeuwes, 2015). Most of these studies however have compared rewarded to unrewarded behavior and did not include different levels of reward. When rewards of different magnitudes can be obtained, saccade endpoints are closer to high than to low reward targets (Bucker, Silvis, Donk, & Theeuwes, 2015) and maximize gain (Schütz et al., 2012), the microsaccade rate scales with value (Yu et al., 2016) and saccade vigor decreases with advanced discounting of rewards (Haith, Reppert, & Shadmehr, 2012; Reppert et al., 2015). Here, looking at saccade latencies without interleaved choices (Experiment 1 & 3), we found no significant evidence for a direct influence of value in two out of three conditions. Bayesian analyses provided evidence for the notion that reward magnitude does not affect latencies in one out of three cases and inconclusive evidence in the remaining two. In Experiment 6, reward influenced baseline levels even without choice-trials. This might point out that latency distributions are more sensitive to reward than average latencies. However, congruent with the average latency differences in the other experiments, modulations of baseline levels were much larger with choice-trials. Thus, in total this suggests that reward alone influences latencies only weakly or not at all. Moreover, the magnitude of reward differences did not modulate latencies (Experiment 1 & 2). This, together with the observation that response delays to less rewarded single-targets can be varied by the amount of inhibition required to perform a reward-maximizing choice (Experiment 4), suggests that participants tried to make an optimal choice, no matter how big the gain or loss.

A previous study (Milstein & Dorris, 2007) reported a linear relation of saccade latency and EV. However, because choice- and single-trials were mixed in this study, it is unclear whether this link would persist in the absence of choices. The here reported inter-trial dependency might also have affected oculomotor and neural findings in monkeys (McCoy, Crowley, Haghighian, Dean, & Platt, 2003; Milstein & Dorris, 2011). A recent study tested whether microsaccade behavior also varies as a function of EV (Yu et al., 2016). The authors reanalyzed their previously collected monkey data mixing choice and single responses (Milstein & Dorris, 2011) and recorded new human data for single-trials only. Both, humans' and monkeys' microsaccades were biased by the

subjective target value. This points out that microsaccades seem to represent value irrespective of whether choices are interleaved or not. Unfortunately, the authors did not report saccade latencies for the human data. This could have been an indication whether or not EV can affect saccade preparation in the absence of interleaved choices.

Our results suggest that target selection modifies subsequent saccade preparation. There is converging evidence that attentional control is not only influenced by stimulus properties (bottom-up) or current goals (top-down), but also by a bias to attend previously selected items (Awh, Belopolsky, & Theeuwes, 2012; Failing & Theeuwes, 2017). For example, inter-trial priming effects seem to require attentional selection (Yashar & Lamy, 2010) and can either be facilitating or inhibitory. Facilitating effects can be observed in visual search when the search target, distractors or their particular features are identical to the preceding trial, leading to shorter reaction times (Maljkovic & Nakayama, 1994; Kristjánsson & Driver, 2008; Feldmann-Wüstefeld & Schubö, 2016). Inhibitory effects occur in conjunction with distractors, for example, saccades curve away from previous distractor locations (Belopolsky & van der Stigchel, 2013) or in the negative priming paradigm, when the identities of target and distractor are exchanged between trials (Neill, 1977). The present study extends findings on inter-trial priming by showing that a selection between two differentially rewarded targets does not facilitate a subsequent response to the chosen one but inhibits a response to the non-chosen one.

We interpret our results in terms of an inhibition of the less rewarded target. Theoretically, the fact that latencies to less rewarded targets increased with an increasing proportion of choices in Experiment 1 does not necessarily imply that these targets are selectively inhibited. Other combinations of several inhibitory and facilitating mechanisms could also explain this pattern: the presence of choices might generally slow down latencies and, simultaneously, selectively speed up responses to highly rewarded targets. In this case, these two mechanisms might cancel each other out for highly rewarded targets, whereas delays towards the less rewarded one would become observable. However, this alternative interpretation seems unlikely because of two other findings: first, the analysis of inter-trial effects showed that responses to less rewarded targets were slowed down after choice-trials, but responses to highly rewarded targets remained unaffected. However, a potential facilitation for highly rewarded targets should have been observable here. Second, the same argument is true for the findings of Experiment 4, where choice-trial difficulty selectively modulated latencies to less but not to highly rewarded targets (Fig 4b). These two findings favor a

selective inhibition of less rewarded targets, but we cannot rule out that other mechanisms are also involved.

Differences between conditions with different proportions of choice-trials (Experiment 1) could theoretically be explained by changes in saccade frequency. Although we cannot dismiss this interpretation, we consider it unlikely, given that latency delays with 25% choice-trials had the same magnitude when we equated saccade frequencies in both directions (Experiment 2). Moreover, studies showing influences of probability on saccade latencies (Carpenter & Williams, 1995; Carpenter, 2004) employ hundreds of trials for every probability condition and dismiss the first 100 trials or more, whereas our blocks in Experiment 1 consisted of only 80 trials.

In Experiment 5 we tested whether our results are influenced by the expectation of an upcoming choice-trial. We cued single-trials to eliminate the expectation of an upcoming choice-trial. If expectation could fully explain our data, latency imbalances should have completely disappeared when upcoming single-trials were cued. However, latency differences were only reduced but not eliminated, suggesting that expectation can only partially explain our findings. Because we only manipulated expectation on a short-term timescale (trial-wise), we cannot exclude the possibility that expectation operating on longer timescales (block-wise) influenced our data but was unaffected by cueing. Nonetheless, our findings cannot be explained by (long-term) expectation alone, given that we found strong inter-trial effects within the same block. However, expectation (short-term and long-term) will have likely added up with inter-trial effects and resulted in delayed saccades to the less rewarded target.

In conclusion, our findings suggest that there is no or only a weak direct connection between reward and saccade preparation to single-targets. A decision between two reward-associated targets leads to a subsequent delay in responses to the non-chosen option. The amount of delay depends on the difficulty to make an optimal, that is, reward-maximizing decision in choice-trials. We propose that these changes in saccade preparation occur due to the subsequent inhibition of the non-chosen target and the expectation of an upcoming choice-trial. This is reflected by a reduced baseline level in the response signal. These results suggest that reward affect saccade preparation particularly if it is behaviorally relevant, for instance if a choice has to be made.

## Methods

*Participants and apparatus*. In total, 47 students from Marburg University aged 19-29 years (M = 23 years) participated in this study (30 female, 17 male). All of them had normal or corrected to normal vision and gave prior informed consent. Participants were paid for participation (8€/h) and received additional reward based on their performance. All experiments were conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and were approved by the local ethics committee LEK FB06 at Giessen university (proposal number 2013-0020). We recorded 25 participants for Experiment 1, 8 participants for Experiment 2, 3 and 5, 12 participants for Experiment 4 and 2 for Experiment 6. Experiments were conducted using the Psychtoolbox (Brainard, 1997) in MATLAB (The Mathworks, Natick, MA, USA) and presented on a VIEWPixx monitor (VPixx Technologies Inc., Saint-Bruno, Quebec, Canada) at a viewing distance of 60 cm. The monitor had a spatial resolution of 1920 × 1080 pixel and a size of 51.5 × 29 cm. We recorded eye movements of the right eye using a desktop mounted EyeLink 1000 (SR Research Ltd., Ontario, Canada) with a sampling rate of 1000 Hz and the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002).

*General methods*. At the beginning of each trial, a black fixation cross with a diameter of 0.5° appeared at screen center on a gray background (Fig. 1). Participants could start trials by pushing the space bar on a keyboard while maintaining fixation. Two crosses (placeholders) with a diameter of 0.25° appeared both left and right from fixation at an eccentricity of 15°. After a random interval (500-1000 ms), the central fixation cross changed its size to 0.25° indicating the onset of the target after additional 600 ms. Targets were dots with a radius of 0.25° and were presented for 500 ms. In single-trials, one dot replaced one of the placeholders, whereas in choice-trials both placeholders were replaced by dots. Participants were instructed to maintain fixation until target appearance and then saccade to a target while it was presented. If they succeeded, their reward for that trial was shown at the target location after target offset. If participants did not make saccades or made saccades to placeholders, they received no reward. Rewards were score points (1, 4, 6 or 9) which were converted into monetary reward at the end of the experiment (1€ for 500 points). At the beginning of each block, participants were informed about the distribution of reward to each hemifield and the relative probability of choice and single-trials. For every experiment, the order of blocks was balanced across participants.

*Experiment 1*. Experiment 1 tested the hypothesis that the effect of reward on saccade latencies in single-trials is modulated by the presence of interleaved choice-trials. We varied the proportion of choice-trials within one block (0%, 25%, 75%). In every block, a fixed reward was assigned to each target/hemifield and rewards were identical for choice- and single-trials. Rewards summed up to 10 score points with one target receiving a higher reward (6 or 9, 'highly rewarded target') than the other (4 or 1, 'less rewarded target'). The reward difference between the two hemifields could be large (1 vs 9) or small (4 vs 6). The experiment thus comprised the three factors (i) choice-trial probability (0%, 25%, 75%), (ii) reward magnitude (highly or less rewarded) and (iii) reward difference (large or small). The trial order was randomized and single-trials to both hemifields appeared equally often. Every combination of choice-trial probability and reward difference was recorded in a block of 80 trials. In total, every participant completed 480 trials and could receive up to 5.60€ reward. The experiment lasted 60-90 minutes.

*Experiment 2*. To show that latency differences caused by choice-trials cannot be explained by a higher saccade probability to highly rewarded targets, we increased the single-trial probability to the less rewarded side. Every participant completed two blocks, one for a small (4 vs 6) and one for a large (1 vs 9) reward difference. Blocks consisted of 120 trials and contained 30 choice-trials (25%). The remaining 90 trials were single-trials, 30 to the highly rewarded and 60 to the less rewarded side. Consequently, participants would saccade equally often to both hemifields if they always chose the highly rewarded target in choice-trials. If they did not, the saccade probability to the less rewarded target would be even higher than 50%.

*Experiment 3*. To test whether the presence of choice-trials modulates or causes the effects of reward on saccade preparation, we changed the reward correspondence between choice- and single-trials. Every participant completed three blocks of 120 trials, all with a high reward difference (1 vs 9). In one block, the highly rewarded side for choice- and single-trials was identical (congruent condition), like in Experiment 1. In another block, the highly rewarded side for choice-trials was the less rewarded side in single-trials (incongruent condition). Both, the congruent and incongruent condition contained 75% of choice-trials. In a third block there were only single-trials.

*Experiment 4*. In order to assess whether the latency modulation due to choices is adaptive, we varied the choice difficulty by changing the contrast of both targets. All targets were darker than the background and Michelson contrasts were 0.5 (black), 0.2 and 0.08. In the difficult condition, the contrast of the highly rewarded target was 0.08 while the other had a contrast of 0.5.

It was the other way round for the easy condition. In the medium condition, both targets had identical contrasts (0.2). The same contrast of 0.2 applied to all fixation crosses, placeholders and targets in single-trials. To make the transition from placeholder to target less salient for the low contrast condition, placeholders remained visible on top of the target during the whole trial for all conditions. Every condition comprised 120 trials. As a manipulation check, we additionally recorded a choice control task and a latency control task. The choice control task consisted of 60 choice-trials without reward but with either the same (0.2) or a different contrast (0.08 vs 0.5). The latency control task consisted of 120 unrewarded single-trials of the three different contrast levels.

*Experiment 5*. To determine whether the effects observed in the previous experiments are caused by the expectation of an upcoming choice-trial, we cued half of the single-trials. The cue was a "1" displayed 1.3° above the central fixation cross. It appeared together with the peripheral placeholders and vanished after 200 ms. The whole experiment consisted of 280 trials, with 50% choice-trials and 25% of cued and uncued single-trials each.

*Experiment 6*. To determine likely neural mechanisms for the interaction of choice- and single-trials, we measured latency distributions to single-trials with (50%) and without choice-trials interleaved and fitted the LATER model(Carpenter & Williams, 1995; Noorani & Carpenter, 2016) to the data. Blocks consisted of 100 trials and participants completed 10 blocks without and 20 blocks with choice-trials (3000 trials in total).

*Data and statistical analysis*. We used the EyeLink 1000 algorithm to determine saccade onsets. Latencies were defined as the first saccadic sample with respect to target onset and successful target choice was defined as the first sample where the gaze was within a square region of 2° around the target. Trials with saccades initiated earlier than 100 ms or later than 450 ms after target onset were not considered for the final analysis of latencies. Across all experiments (apart from Experiment 4 where missing the target was a dependent variable), this happened in 1.59% of trials. Due to technical issues, some eye movement traces could not be saved in 2.99% of trials. These recording errors were evenly distributed across all experiments and conditions.

Normality of the data was assessed by Kolmogorov-Smirnov tests and by visually inspecting Q-Q-plots. Statistical tests on saccade latencies in Experiment 1-4 were done using repeated-measures ANOVA and post-hoc t-tests with Bonferroni-corrected $\alpha$ level. If sphericity was violated, we report corrected p-values according to Greenhouse-Geisser. We supplemented our analyses with Bayes factors (Rouder, Speckman, Sun, Morey, & Iverson, 2009) (BF) when

non-significant results were crucially relevant for interpreting the data. BFs were computed in R (3.3.2; R Development Core Team, 2016) using the *BayesFactor* package with default priors. BFs smaller one favor the null hypothesis and values greater one favor the alternative hypothesis. Evidence is stronger, the further BFs deviate from 1, with values between 0.33 and 3 being considered inconclusive evidence (Jeffreys, 1961). In Experiment 5, we compared latency differences using Wilcoxon signed-rank tests, because the data were not normally distributed. Performance values in Experiment 4 were compared using the non-parametrical Friedman test. Analyses were carried out in MATLAB, R and SPSS (Version 22, IBM Corp., Armonk, NY).

*Choice-trial behavior.* In all experiments, we varied the presence of choice-trials as independent variable without being interested in the participants' behavior in these trials. In choice-trials, participants almost always chose the target with the higher reward (e.g. in Experiment 1: M = 95.3%, SD = 2.5%; Experiment 3: M = 95%, SD = 3.1%) with similar latencies as in single-trials without choice-trials (Experiment 1: M = 214 ms, SD = 22 ms) or slightly elevated (Experiment 3: M = 224, SD = 22ms).

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**Author Contributions**

C.W., A.H., A.S. and A.C.S. conceived and designed the research. C.W and A.C.S. analyzed the data. C.W. and A.C.S. wrote the first draft of the manuscript. All authors revised the manuscript.

**Additional Information**

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## Author contributions

**Study I**

Wolf, C., & Schütz, A.C. (2017). Earlier saccades to task-relevant targets irrespective of relative gain between peripheral and foveal information. *Journal of Vision*, *17*(6):21, 1-18. doi:10.1167/17.6.21

CW and ACS designed the research. CW collected and analyzed the data. CW wrote the first draft of the manuscript. CW and ACS revised the manuscript.

CW: 75%, ACS: 25%

**Study II**

Wolf, C., & Schütz, A.C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision*, *16*(16):1, 1-18. doi:10.1167/15.16.1

CW and ACS designed the research. CW collected and analyzed the data. CW and ACS wrote and revised the manuscript.

CW: 75%, ACS: 25%

**Study III**

Wolf, C., Heuer, A., Schubö, A., & Schütz, A.C. (submitted). The necessity to choose causes the effects of reward on saccade preparation.

CW, AH, AS and ACS designed the experiments. CW recorded the data. CW and ACS analyzed the data. CW wrote the first draft of the manuscript, all authors revised the manuscript.

CW: 50%, AH: 10%, AS: 10%, ACS: 30%

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## Zusammenfassung

Nur mit dem zentralen Punkt der Netzhaut, der Fovea, können wir feine Details unserer visuellen Umgebung erkennen. In der Peripherie hingegen nimmt die Auflösung mit zunehmender Exzentrizität ab. Folglich bewegen Menschen ihre Augen, um mit den beiden Foveae hochauflösende Information über relevante und interessante Dinge zu erhalten. Mit jeder dieser sakkadischen Augenbewegungen entscheiden wir uns dafür, einen bestimmten Bereich unserer Umwelt genauer zu inspizieren. Daher, und weil das Blickbewegungssystem beeinflusst wird durch Belohnungs- und Bewertungsprozesse, hat sich in den letzten Jahren die Forschung zu Entscheidungsfindung zunehmend auf das Blickbewegungssystem konzentriert (Glimcher, 2003). Augenbewegungen sind aber nicht nur aufschlussreich in Bezug auf Entscheidungsfindung, sondern auch in Bezug auf visuelle Wahrnehmung, denn die beiden sind untrennbar miteinander verbunden: Wo wir hinschauen, bestimmt, was wir sehen und jede Augenbewegung stellt das Sehsystem vor eine Herausforderung, da die visuelle Information auf der Netzhaut verschoben wird. Die vorliegende Dissertation untersuchte in drei Studien, ob das Blickbewegungssystem Sakkadenlatenzen anpassen kann, um visuelle Informationen optimal aufzunehmen und Belohnung zu maximieren, und ob das Sehsystem alle ihm zur Verfügung stehenden visuellen Information nutzen kann, obwohl diese von einer Augenbewegung getrennt ist.

Die erste Studie untersuchte, ob das Blickbewegungssystem sensitiv ist für die Information, die durch Ausführung einer Sakkade gewonnen wird. Versuchspersonen schauten zu einem Ziel in der Peripherie um dort eine Wahrnehmungsaufgabe auszuführen. Durch Austauschen des Ziels während der Sakkade, konnten wir die periphere und foveale Sichtbarkeit unabhängig voneinander manipulieren und Bedingungen kreieren, in denen die Versuchspersonen durch eine Augenbewegung Informationen verloren oder gewonnen. In der Verlust-Bedingung stieg die Diskriminationsleistung mit zunehmender Latenz an, da Versuchspersonen länger von der hohen peripheren Sichtbarkeit profitieren konnten. Umgekehrt, zeigte sich in der Gewinn-Bedingung eine bessere Performanz für kürzere Latenzen. Jedoch zeigte sich kein Unterschied in den Latenzen der beiden Bedingungen, so dass Latenzen nicht angepasst wurden, um den Informationswert zu maximieren. Stattdessen sanken Latenzen mit zunehmender Wahrscheinlichkeit, dass das Sakkadenziel aufgabenrelevant ist. Dies legt nahe, dass die Motivation aufgabenrelevante

Information zu fovealisieren, Sakkadenlatenzen moduliert, jedoch nicht der Informationsgewinn, der mit einer Sakkade einhergeht.

Studie II untersuchte, ob das Sehsystem in der Lage ist, prä-sakkadische periphere und post-sakkadische foveale Information zu integrieren und die beiden gemäß ihrer Reliabilität gewichtet, das heißt gemäß ihrer Sichtbarkeit. Eine solche optimale Integration würde die perzeptuelle Unsicherheit minimieren und daher alle zur Verfügung stehenden Informationen maximieren. Für jede Versuchsperson wurde separat die Diskriminationsfähigkeit in der Fovea und Peripherie gemessen. Mittels Maximum-Likelihood Estimation (Ernst & Bülthoff, 2004) konnten wir daraus für jede Person die optimale Gewichtung bestimmen, die der peripheren Information zukommen sollte, wie auch die minimale Unsicherheit des optimalen trans-sakkadischen Perzepts. Sowohl die gemessen Gewichtung als auch die Unsicherheit unterschieden sich nicht von den Werten, die durch optimale Integration vorhergesagt wurden. Wir konnten also zeigen, dass das Sehsystem in der Lage ist, Informationen über Sakkaden hinweg zu integrieren und dass es dabei nahezu optimal ist. Dies legt nahe, dass das Sehsystem die ihm zur Verfügung stehenden Informationen trotz Augenbewegungen optimal nutzen kann.

Studie III beschäftigte sich damit, ob sich der Einfluss erwarteten Motivationswertes auf Sakkaden (Milstein & Dorris, 2007, 2011) nur in Kontexten zeigt, in denen Versuchspersonen zusätzlich zwischen verschiedenen belohnten Zielen wählen können. Abhängige Variable waren Latenzen zu einzelnen Zielen unterschiedlicher Belohnungshöhe, unabhängige Variable war der Anteil an Auswahldurchgängen innerhalb eines Blocks. In Auswahldurchgängen wurden zwei Ziele dargeboten und die Versuchspersonen konnten sich entscheiden, zu welchem sie hinschauen, um entweder die hohe oder die niedrige Belohnung zu erhalten. In Blocks ohne Auswahl fand sich keine Evidenz für einen Einfluss von Belohnung auf Sakkadenlatenzen. In Blocks, in denen Auswahldurchgänge durchmischt waren, waren Latenzen zum niedriger belohnten Ziel erhöht. Diese verzögerten Latenzen wurden durch die Erwartung eines Auswahldurchgangs hervorgerufen als auch durch *inter-trial priming*: Nach einem Auswahldurchgang, waren Sakkaden zu jenem Einzeltarget verlangsamt, das zuvor nicht ausgewählt wurde. Wir konnten folglich zeigen, dass es keinen direkten Zusammenhang zwischen Sakkadenlatenzen auf der einen und Belohnungswert auf der anderen Seite gibt. Stattdessen zeigt sich dieser Zusammenhang nur in Kontexten, in dem Personen mit ihrem Verhalten einen direkten Einfluss auf die Belohnungshöhe haben und ihre Belohnung maximieren können, indem sie ein Ziel dem anderen bevorzugen.

Zusammengefasst zeigt die vorliegende Dissertation, dass es keinen direkten Zusammenhang zwischen Sakkadenlatenzen auf der einen und Informationswert (Studie I) oder Motivationswert (Studie III) auf der anderen Seite gibt. Stattdessen werden Sakkadenlatenzen moduliert durch die Wahrscheinlichkeit, aufgabenrelevante Information zu fovealisieren (Studie I) sowie durch die Bevorzugung eines Ziels gegenüber eines anderen (Studie III). Für die Wahrnehmung konnten wir zeigen, dass das Sehsystem Informationen über Sakkaden hinweg integrieren kann (Study II) und dass unsere visuelle Wahrnehmung somit nicht aus einzelnen Schnappschüssen besteht, sondern aus einem kontinuierlichen, integrierten Strom visueller Informationen.

## Erklärung

Hiermit versichere ich, die vorliegende Dissertation

*Eye movements and the maximization of value*

selbstständig angefertigt zu haben. Ich habe mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient und alle vollständig oder sinngemäß wiedergegebenen Zitate als solche gekennzeichnet.

Ich habe früher noch keine Promotion an der Philipps-Universität Marburg oder an einer anderen Universität eingereicht. Auch die vorliegende Dissertation wurde weder in ihrer jetzigen noch in einer ähnlichen Form bei einer anderen Hochschule eingereicht und hat noch keinen Prüfungszwecken gedient.

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(Christian Wolf)